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A REVISION OF THE GENERA *DICRANUM* AND *ORTHODICRANUM* (MUSCI) IN NORTH AMERICA NORTH OF MEXICO

by

© WILBUR PETERSON

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY
IN
BRYOLOGY

DEPARTMENT OF BOTANY
EDMONTON, ALBERTA
SPRING, 1979

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "A Revision of the Genera Dicranum and Orthodicranum (Musci) in North America North of Mexico" submitted by Wilbur Peterson in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Bryology.

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ABSTRACT

The genera *Dicranum* and *Orthodicranum* are revised for North America north of Mexico, with twenty-one species and one variety recognized in the former and five species recognized in the latter. Six taxa (*D. condensatum*, *D. ontariense*, *D. pallidisetum*, *D. sulcatum*, *D. rhabdocarpum and D. brevifolium* var. *bistratosum*) are considered endemic to North America. *Dicranum brevifolium var. bistratosum* is described as new and *D. amannii* is recognized as new to the flora of North America. Several nomenclature changes are made; *Dicranum ontariense* Peterson is the correct name for the endemic taxon previously termed *D. drummondii* C. Müll.; *Dicranum condensatum* Hedw. is the correct name for specimens called *D. sabuletorum* Ren. & Card.; *Dicranum amannii* Peterson *nom. nov.* is proposed for the illegitimate *D. latifolium* Amann; *Orthodicranum strictum* is attributed to Culmann, not Schleicher; *Dicranum majus* is attributed to Smith, not Turner; and the name *D. sulcatum* Kindb. is recognized for the specimens of the section *Fuscescentiformia* which have a long-excurrent costa and grow on logs and living trees in the coniferous forest region of the west coast. Descriptions, ecological data, distribution maps, drawings, and short discussions of distinguishing features are presented for all taxa. As well, each taxon is typified, a list of synonymy is given and a composite key is presented.

Morphological, phytogeographical, ecological and cytological data suggest the recognition of two genera, *Orthodicranum* and *Dicranum*, with the latter segregated into five sections; *Dicranum*, *Fuscescentiformia*, *Elongata*, *Spuria*, and *Muehlenbeckia*. The latter is described as new. Phenetic and phylogenetic analyses in the form of taxometric maps and a "Wagner Tree" support this segregation. The phytogeography of the species suggests the group to be an ancient one, probably evolving in the early Tertiary. The distribution patterns support the hypothesis that moss species are subject to the same distributional pressures as vascular plants. The Pleistocene glaciations and the orogeny of the Rocky Mountains were the most significant influences upon the distributions of the species, while continental drift is used to explain the distribution pattern of *D. leioneuron* and long distance dispersal is the probable cause for the occurrence of *D. scoparium* in New Zealand.

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INTRODUCTION

The Changes in Generic Concept

The moss genus *Dicranum* was first described by Hedwig (1782) and nomenclaturally dates from Hedwig (1801). It is one of 48 genera in the Dicranaceae (Brotherus, 1924) and was originally characterized (Hedwig, 1801) by 1) an erect habit with terminal sporophytes, 2) a single row of peristome teeth, and 3) divided peristome teeth. Of Hedwig's (1801) thirty-four original species, only three (*Dicranum condensatum*, *D. scoparium*, and *D. spurium*) remain within the modern concept of the genus. According to Wijk *et al.* (1962), the remainder can be recognized under sixteen different genera, with nine in *Dicranella*, four in *Ceratodon*, three in *Campylopus*, two each in *Anisothecium*, and *Orthodicranum*, and one in each of *Dicranoloma Kiaeria*, *Paraleucobryum*, *Leucobryum*, *Oncophorus*, *Ditrichum*, *Desmatodon*, *Dichodontium*, *Grimmia*, *Rhacomitrium* and *Weisia*. The establishment of these genera has narrowed Hedwig's original concept considerably.

New genera within the Dicranaceae have been established according to modifications in one or more of approximately six characters. Bridel (1819) established the genus *Campylopus* based on curved setae and nodding capsules. Members of this genus also have a very wide costa that occupies

1/2 to 9/10 the width of the leaf base, and the capsules lack the stomates that normally occur in most mosses. In turn, segregation of the genus *Campylopus* has been based on the entire peristome as in the cases of *Pilopogon* (Bridel, 1826) and *Thysanomitrium* (Schwaegrichen, 1823), and degrees of cellular differentation within the costa in the cases of *Brothera* (Müller, 1901) and *Paraleucobryum* (Loeske, 1910). *Thysanomitrium* differs from *Pilopogon* chiefly by an elliptic, exannulate capsule. *Brothera* has thin-walled cells on both adaxial and abaxial surfaces of the costa with stereid cells and guide cells in between, while *Campylopus* has thin-walled cells on only the adaxial surface with guide cells and stereid cells composing the remainder. *Paraleucobryum* has large lumened cells throughout the costa (i.e. no stereids or well defined guide cells). Other genera of the *Campylopus* complex are *Dicranodontium* (Bruch, Schimper, and Gümbel, 1847) and *Atractylocarpus* (Mitten, 1869). Although *Atractylocarpus* has straight setae, its relationship to *Campylopus* is evident in the width of the costa and its internal leaf anatomy.

The absence of differentiated alar cells led to the separation of *Aongstroemia* (Bruch, Schimper, and Gümbel, 1847) and *Dicranella* (Schimper, 1856), while an autoicous sexual state along with other such characters as peristome insertion, sheathing leaf bases and a lack of internal costa differentation formed the basis for *Holomitrium* (Bridel, 1826), *Oncophorus* (Bridel, 1826), and *Arctoa* (Bruch, Schimper, and Gümbel, 1847). *Oncophorus* was later divided into two genera, *Onocophorus* and *Cynodontium* (Schimper, 1856), with the former having curved capsules and the latter having erect capsules. Hagen (1915) acted similarly by segregating *Kiaeria* (curved capsules) from *Arctoa* (straight capsules). Hagen also established another segregate from *Cynodontium*, the genus *Cnestrum*, because of stalked perigonia and undivided peristome teeth. The genus *Orthodicranum* (Loeske, 1910) was also established on the basis of straight capsules. The degree to which each peristome tooth is split was instrumental in the establishment of *Ditrichum* (Hampe, 1867) and *Ceratodon* (Bridel, 1826), both having teeth split nearly to the base. These two genera are now considered members of a separate family, the Ditrichaceae. This is supported cytologically since the base number for the Ditrichaceae is n=13 while that of the Dicranaceae is mostly x=14 and x=12 (Steere, 1972).

This narrowing of generic concepts gained acceptance among bryologists and became evident in the major bryological treatments. Bruch, Schimper, and Gümbel in their *Bryologia Europaea* (1847) recognized seven genera (*Arctoa*, *Aongstroemia*, *Campylopus*, *Cynodontium*, *Dicranodontium*, *Trematodon*, and *Dicranum*) in the Dicranaceae with eleven sections under the genus *Dicranum*. These sections include species now considered as members of *Oncophorus*, *Dicranella*, *Arctoa*, *Orthodicranum*, and *Paraleucobryum*. In contrast, Carl Müller in his *Synopsis Muscorum Frondosorum* (1848) published one year after Bruch, Schimper, and Gümbel's Dicranaceae treatment, presented a more conservative view. He listed 6 genera within the Dicranaceae (*Blindia*, *Dicranum*, *Dicnemon*, *Eucamptodon*, *Holomitrium*, and *Pilopogum*) with all but *Dicranum* and *Blindia* occurring in the tropics or Southern Hemisphere.

Under the genus *Dicranum* he recognized five sections (*Dicranum*, *Campylopus*, *Leucoloma*, *Onocophorus*, and *Orthodicranum*). All of these are presently considered generically sound by most modern authors. It is evident disharmony existed in generic concepts when two major publications appeared this close together with one recognizing 6 genera in the world and the other 7 genera in Europe. The proliferation of genera in the Dicranaceae by the elevation of sections was again evident in Brotherus' treatment of the Musci in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (1906) in which 44 genera were recognized in the Dicranaceae. This treatment was in marked contrast to that of Müller (1848). Brotherus did retain *Arctoa*, *Chorisodontium*, *Holodontium*, *Leiodicranum*, *Crassidicranum*, and *Paraleucobryum* as subgenera of *Dicranum* and *Orthodicranum* as a section; however, in the 1924-25 edition of Engler and Prantl, Brotherus elevated all of these except for *Leiodicranum* and *Crassidicranum*. *Paraleucobryum* was elevated to the sub-family Paraleucobryoideae and the rest were elevated to the generic level. In addition, the 1906 sections *Dicranoloma* (under *Leucoloma*) and *Thysanomitrium* (under *Campylopus*) were elevated to generic status and the "Unterfamilien" Ditricheae, Seligerieae, Bryoxipheae, and Dicnemoneae were elevated to the familial level, becoming the Ditrichaceae, Seligeriaceae, Bryoxiphiaceae, and Dicnemonaceae respectively. In total, Brotherus expanded the one family with 44 genera under his 1906 concept to five families and 76 genera in his 1924 concept, with the Dicranaceae containing 48 genera and the genus *Dicranum* composed of 3 subgenera (*Eudicranum*, *Crassidicranum*, and

Pseudochorisodontium).

This narrow generic concept of *Dicranum* has been maintained by recent European bryologists (Nyholm, 1954; Podpera, 1954, Savicz-Ljubitzkaja, and Smirnova, 1970) while North American bryologists have returned to a somewhat more conservative concept by reuniting *Orthodicranum* with *Dicranum* (Grout, 1937; Lawton, 1971; Crum, 1973; Flowers, 1973). Considerable differences exist between *Orthodicranum* and *Dicranum* as shown in Table 1. All species of *Orthodicranum* possess this combination of character states (except for infrequent asexual reproduction in *O. montanum*). Some *Dicranum* species, such as *D. groenlandicum*, do have some of these character states. *Dicranum groenlandicum* has erect capsules; however, the capsules are ribbed, the alar region is bistratose and it has a habitat of soil or humus. *Dicranum fragilifolium* has specialized asexual reproduction in the form of broken leaf tips, but it also has a curved ribbed capsule and a bistratose alar region. *Dicranum rhabdocarpum*, an intermediate species because of semi-erect capsules and bistratose spots in the alar region (see Discussion under *D. rhabdocarpum*) has been placed under *Orthodicranum* by some (Holzinger, 1925; Podpera, 1954); however, in agreement with Steere (1947), I believe an intermediate species should remain with the more inclusive concept of the older genus. If this species is not included within *Orthodicranum* the genus is sharply delimited from the genus *Dicranum*. The characters in Table 1 are from both sporophytic and gametophytic generations and unify *Orthodicranum* into a concise group that should not be denied the status of genus. I

TABLE 1. Differences between *Orthodicranum* and *Dicranum*

Orthodicranum	*Dicranum*
1. Capsules straight	1. Capsules curved
2. Capsules smooth to slightly wrinkled	2. Capsules ribbed
3. Alar cell region unistratose	3. Alar cell region bistratose
4. Peristome teeth relatively narrow (<60 μm)	4. Peristome teeth relatively wide (70-95 μm or more)
5. Specialized asexual reproduction by broken leaf tips or flagellated branches common	5. Specialized asexual reproduction rare.
6. Specialized habitat of rocks and wood	6. Habitat of wood or rock rare, usually on soil or humus

am considering it as such and, because of its close relationship to *Dicranum*, I am treating it along with *Dicranum*.

Present day bryologists working in the Southern Hemisphere (Sainsbury, 1955; Scott, Stone, and Rosser, 1976) and the Tropics (Whitter, 1976) have also adopted the narrow generic concept of Brotherus (1924). Under the modern concept, *Dicranum* is distributed mostly in the north temperate regions of the world (Fig. 1) with its relatives *Campylopus* (Fig. 2), *Dicranoloma* (Fig.3), and *Chorisodontium* (Fig. 3) often filling the same ecological niches in the tropics and southern hemisphere. *Chorisodontium* (Brotherus, 1924) is geographically restricted to South America and southern Africa and differs most conspicuously by having precociously germinating spores. *Dicranoloma*, which was segregated from *Leucoloma* (Renauld, 1901), has been accepted as a distinct genus in the southern hemisphere by Sainsbury (1955), Scott, Stone, and Rosser (1976), and Whitter (1976), because of a very narrow costa and smooth cells, while *Leucoloma* has a wider costa and papillose cells. Both have a leaf border of elongated, hyaline cells which has been used to separate the latter from the few members of *Dicranum* which occur in the southern hemisphere. *Dicranoloma* does have representatives that occur in Mexico (Williams, 1913), Hawaii (Bartram, 1933), and as far north as Japan (Takaki, 1966). In these distributional extremes the species often appear quite similar to *Dicranum scoparium* since the hyaline leaf border that serves as an identification character in southern hemisphere specimens is weak or absent (Takaki, 1966). Takaki emphasized the narrow costa and the peristome teeth that are short and

FIGURE 1. Numbers of *Dicranum* species reported from the major geographic regions of the world, according to Wijk *et al.* (1962).

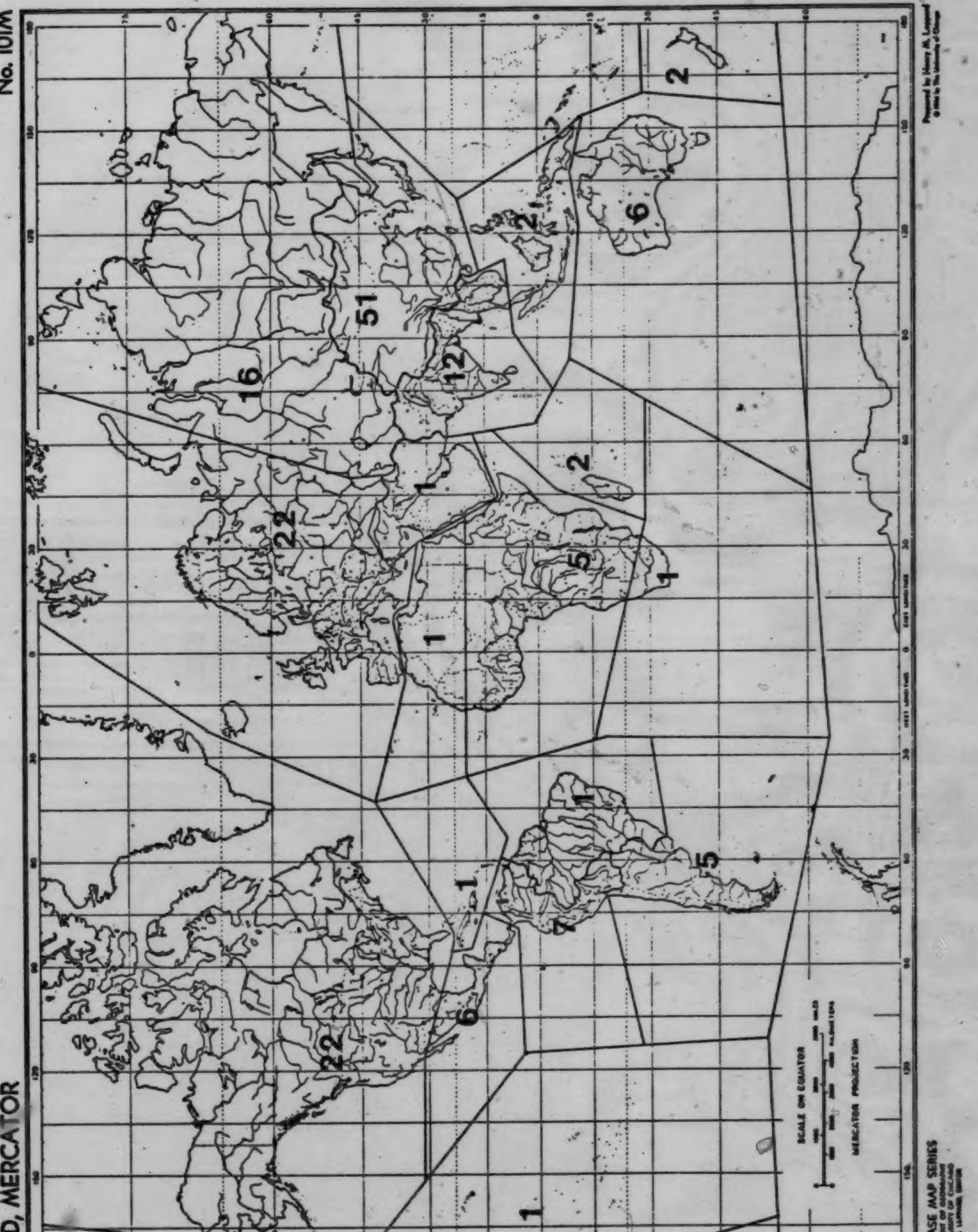

WORLD, MERCATOR
No. 101M
22
6
1
7
1
5
1
1
22
5
1
2
1
16
51
12
2
6
2
1
SCALE ON EQUATOR
MERCATOR PROJECTION
GOODE BASE MAP SERIES
Prepared by Henry M. Leppard

FIGURE 2. Numbers of *Campylopus* species reported from the major geographic regions of the world, according to Wijk *et al.* (1962).

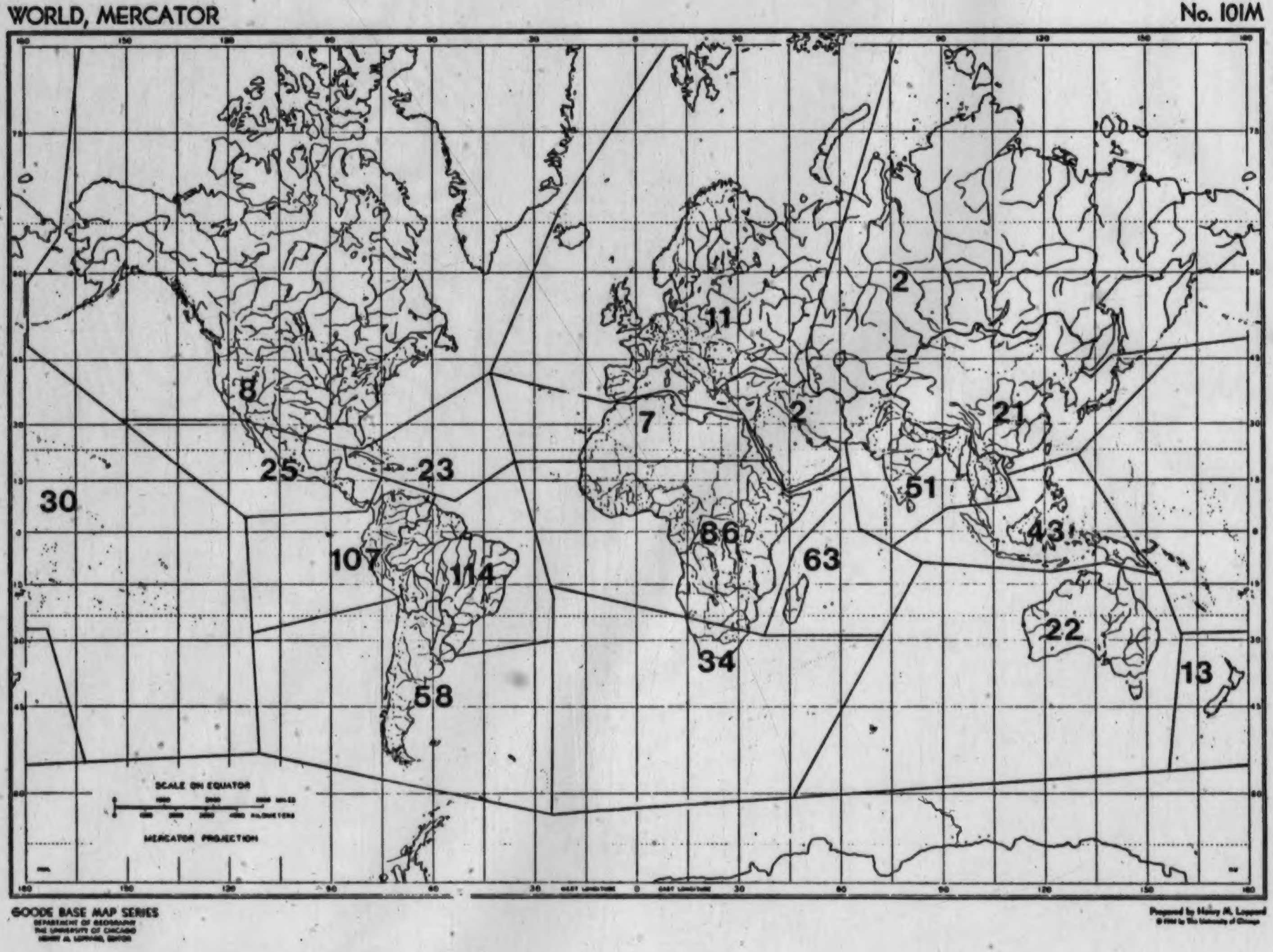
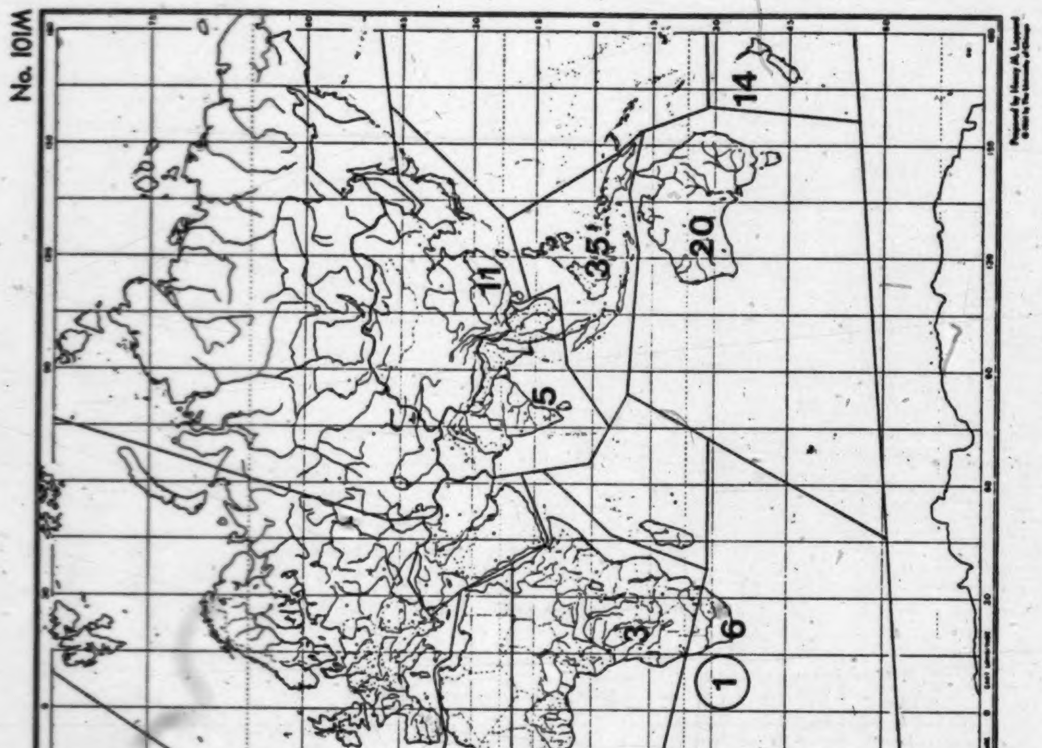

WORLD, MERCATOR
No. 101M
2
11
2
21
8
7
25
23
30
51
43
86
63
107
114
22
34
13
58
SCALE ON EQUATOR
MERCATOR PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard

FIGURE 3. Numbers of *Dicranoloma* and *Chorisodontium* (circled numbers) species reported from the major geographic regions of the world according to Wijk *et al.* (1962).


WORLD, MERCATOR
No. 101M
22
1
2
5
5
18
3
3
1
6
5
11
35
20
14
SCALE ON EQUATOR
MERCATOR PROJECTION
GOODE BASE MAP SERIES

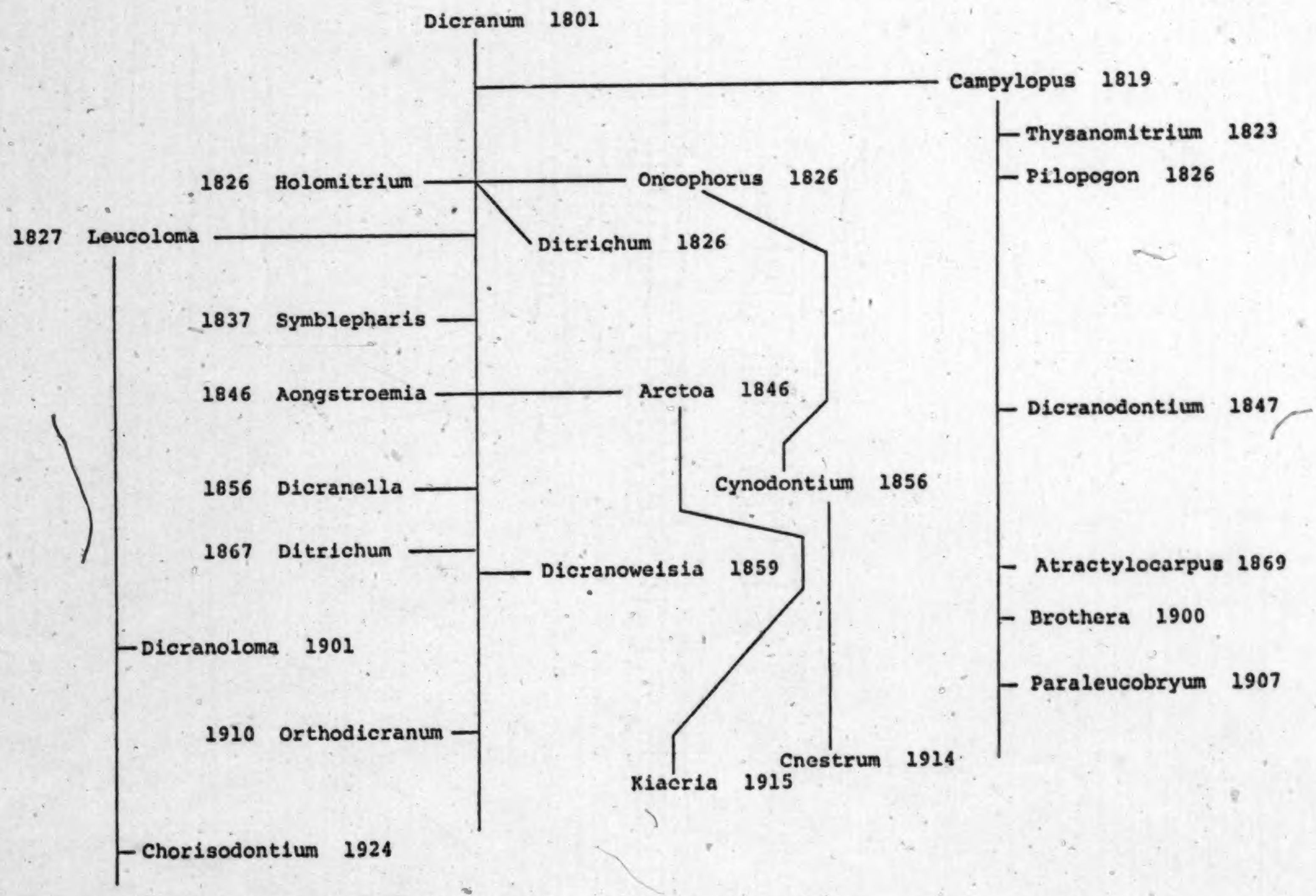
divided into obtusesegments in his treatment, as well as pointing out that the long "incrassate" cells between the costa and the alar region are diagnostic in Japanese species. These character states are diagnostic for the genus and to these can be added the sporophytic characters of long, erect to semi-erect capsules with firm, smooth walls. Most of these characters are sporophytic and it is understandable why sterile specimens might be placed under *Dicranum*; however, the absence of usable characters in the gametophyte does not negate the validity of the genus.

Arctoa and *Kiaeria*, two members of the Dicranaceae found in North America (usually arctic or alpine) are gametophytically difficult to distinguish from the genus *Dicranum*. Williams (1913) treated both of these genera under the *Dicranum* section *Arctoa*; however, most authors since have recognized the genus *Arctoa* s.l. as being distinct (Brotherus 1924; Nyholm, 1954; Takaki, 1964; Lawton, 1971; Crum *et al.*, 1973). *Kiaeria* is distinguished from *Arctoa* by a curved, somewhat strumose capsule and smaller spores. The two genera are virtually inseparable when sterile; however, they are still easily distinguished from the genus *Dicranum* s.str. The gametophytic characters that have been used to place sterile specimens in either *Arctoa* or *Kiaeria* are the 'homogeneous' anatomy of the costa, and the lack of well differentiated alar cells (Williams, 1913; Lawton, 1971). The term 'homogeneous' is a misnomer in this case since all species do have enlarged guide cells (sometimes only in the lower half of the leaf) that are quite different from the surrounding cells. Still, there is not the degree of costal differentiation that is found in *Dicranum* s.str. and neither *Arctoa* nor *Kiaeria* possess bands of stereid cells. The alar cells of *Arctoa* and *Kiaeria* are often dark in colour, thus giving the illusion of being well developed, but they are never highly inflated as in *Dicranum* s.str. and they are usually indistinctly set off from the lower laminal cells. In addition, many seemingly sterile specimens of *Arctoa* and *Kiaeria* actually have well hidden archegonia and antheridia, and confirmation of the autoicous condition is possible.

Today, after the establishment and acceptance of the previously mentioned generic concepts (Fig. 4), we are left with a narrow definition for *Dicranum* s.str. which can be outlined as possessing a combination of the following character states:

1. Terminal sporophytes (Acrocarpous) and erect habit
2. Dioicous
3. Alar cells well differentiated
4. Alar region bistratose
5. Costa narrow, filling about 1/5 of the leaf base
6. Absence of a strong border of hyaline cells on the leaves.
7. Curved capsules
8. Ribbed capsules
9. Haplolepideous peristome
10. Peristome teeth divided approximately half way to the base

FIGURE 4. The major genera that have been segregated from Hedwig's original concept of the genus *Dicranum*.


Dicranum 1801
Campylopus 1819
Thysanomitrium 1823
Pilopogon 1826
1826 Holomitrium
Oncophorus 1826
1827 Leucoloma
Ditrichum 1826
1837 Symblepharis
1846 Aongstroemia
Arctoa 1846
Dicranodontium 1847
1856 Dicranella
Cynodontium 1856
1867 Ditrichum
Dicranoweisia 1859
Atractylocarpus 1869
Brothera 1900
Dicranoloma 1901
Paraleucobryum 1907
1910 Orthodicranum
Cnestrum 1914
Kiacria 1915
Chorisodontium 1924

Recent History of North American *Dicranum* Species

North American Dicrana have not been critically examined, except for a few species, since Williams (1913) treated the family Dicranaceae. Williams recognized thirty-six species of *Dicranum* in North America including 8 species in the section *Arctoa*, 5 species in the section *Orthodicranum*, 3 species in the section *Paraleucobryum*, and 20 species in the section *Eudicranum*. One species, *Dicranum laevidens*, was described as new. Grout (1937) followed the concepts of Williams, with a few modifications, and his work is still used as a major reference source by most North American bryologists. Prior to the work of Williams (1913), North American Dicrana were studied by such bryologists as Renauld and Cardot (Cardot, 1899; Renauld and Cardot, 1888, 1889) who described *D. sabuletorum*, Sullivant (1849, 1856) who described *D. rhabdocarpum*, True (1899) who was interested in geographical distribution of the species, and Barnes (1890) who studied the relationships of several varieties of *D. bonjeanii*.

John Macoun was an important North American collector of mosses; however, he sent most of his material to Kindberg, a Swedish bryologist, for identification. This resulted in the description of 48 new taxa within *Dicranum* (Kindberg, 1889, 1890, 1896, 1897, 1905, 1910; Macoun, 1889, 1890a, 1890b, 1892; Röll, 1896). Most of these species have been placed in synonymy with older names, but the larger number of taxa, mostly from western North America , suggests a complexity in this geographic region that does not exist elsewhere in North America (Crum, 1973). Most of these species were, no doubt, described from one or two specimens and Kindberg was unable to see the range of variation displayed by many of the characters. It is unfortunate that this happened, because all Kindberg and Macoun species are now regarded with suspicion, when actually several of them are as distinct as species described by other authors.

Taxonomically, very little has been done with the North American Dicrana since the Williams' (1913) work. *Dicranum pallidisetum* has been elevated to specific level by Ireland (1965), who at the same time suggested that the anatomy of the costa as seen in transverse-section might be of major importance in determining many or all *Dicranum* species. Also, I have published two papers on nomenclature, confirming the validity of the name *D. condensatum* Hedw. over *D. sabuletorum* Ren. and Card. (Peterson, 1977a) and providing a new name for the North American endemic (*D. ontariense*) that was technically without a name but referred to as *D. drummondii* C.M. (Peterson, 1977b). European Dicrana have had little taxonomic consideration. Hagen's (1915) work on Norwegian Dicranaceae was significant in that he segregated *D. flagellare* and *D. montanum* into the genus *Scytalina* and *Kiaeria* from *Arctoa*. Other contributions to *Dicranum* include Amann (1912), who described *D. latifolium*, Podpera (1954), who segregated several species into *Orthodicranum*, Nyholm, who's *Illustrated Moss Flora of Fennoscandia* (1954) is an excellent treatment dealing with the more northern species, Briggs (1965a), who critically examined four species of *Dicranum* found in England, and Hegewald's (1968, 1972a, 1972b, 1972c) work on *Dicranum* *scoparium* f. *saltans*, *D. tauricum*, and *D. viride* in Germany and *D. groenlandicum* in Finland.

Recent works dealing with *Dicranum* are usually concerned with ecology, as that of Ahti and Isoviita (1962) and Ahti *et al.* (1965) on the occurrence of *D. leioneuron* in ombrotrophic bogs, Briggs (1965b) who studied the ecology of four *Dicranum* species in England, Seltzer and Wistendahl (1971) who investigated environmental factors affecting *D. fulvum*, and Tarkhova (1970) who examined soil factors affecting the development of several moss species including *D. polysetum*. Physiological and developmental studies have been recently conducted too. Klepper (1963) and Peterson and Mayo (1975) examined water relations in *D. scoparium* and *D. polysetum* respectively. Hicklenton and Oechel (1976) studied the physiology of *D. fuscescens* in the subarctic, Loveland (1956) studied sexual dimorphism in *Dicranum*, Chrobak and Sharp (1965) compared asexual reproduction in two *Dicranum* species, and Valanne *et al.* (1976) studied ultrastructural changes in germinating spores. Geographic distributional studies dealing specifically with *Dicranum* (Takaki, 1972) and studies including *Dicranum* (LaRoi and Stringer, 1976) have been conducted and almost all floristic treatments include some Dicrana within their geographical limits (Lawton, 1971; Crum, 1973; Flowers, 1973; Vitt, 1975).

No complete cytological study has been attempted on *Dicranum* as material in the proper stage is difficult to obtain; however, a number of counts have been made (Anderson and Bryan, 1958; Anderson and Crum, 1958; Anderson, 1962; Briggs, 1965a, Bryan, 1956; Ireland, 1965; Steere, 1954, 1972; Vaarama, 1950; Yano, 1950, 1957). The counts found (Table 2) reflect a basic number of X=12 with a few variations. This base number differs from other genera in the Dicranaceae such as *Dicranella* and *Cynodontium* which have a base number of X=14. In addition, these base numbers of X=12 and X=14 in the Dicranaceae support the segregation of the family Ditrichaceae which has a base number of X=13 (Anderson and Crum, 1958). Polyploids have been found in three instances, for *Orthodicranum flagellare* (n=12, n=23), *Dicranum brevifolium* (n=12, n=24), and *D. spurium* (n=12, n=24). In addition, one collection of *Dicranum fuscescens* from North Carolina has been found with a chromosome complement of n=8 (Anderson, *pers. comm.*). According to Steere (1972), such numbers as n=8 are probably the result of reduction from the more common n=12 situation. Other counts (n=11, n=13, n=14, n=15, n=17) have been recorded and might be a function of small "m" chromosomes that may not be seen when making counts from gametophytic tissue (Anderson and Crum, 1958).

TABLE 2. Chromosome numbers reported for species of *Dicranum* and *Orthodicranum* that occur in North America.

SPECIES	CHROMOSOME NUMBER	SOURCE LOCALITY	REFERENCE
Dicranum brevifolium Lindb. (as *D. fuscescens*)	n=12	Alberta	Anderson & Crum, 1958
	n=24	Alberta	Anderson & Crum, 1958
Dicranum condensatum Hedw.	n=12	North Carolina	Bryan, 1956
Dicranum elongatum Schleich. *ex* Schwaegr.	n=12	Alaska	Steere, 1954
Dicranum groenlandicum Brid.	n=12	Alberta	Anderson & Crum, 1958
Dicranum majus Sm.	n=11	Japan	Yano, 1950, 1951
	n=12	Alaska	Steere, 1954
	n=17 (12+5)	Finland	Vaarama, 1950a
Dicranum pallidisetum (Bail. *ex* Holz) Irel.	n=12	Washington	Ireland, 1965
Dicranum polysetum Sw.	n=11	Japan	Yano, 1951
	n=12	Finland	Vaarama, 1950b
	n=13 (12+1)	Denmark	Holmen, 1958
Dicranum scoparium Hedw.	n=11	Japan	Yano, 1954
	n=12	North Carolina	Anderson & Bryan, 1958
	n=12	Michigan	Snider, 1970
Dicranum spadiceum Zett.	n=12		Anderson & Bryan, 1958
Dicranum spurium Hedw.	n=12	Finland	Vaarama, 1950b
	n=24		Crum, 1973
	n=12	Michigan	Snider, 1970
Orthodicranum flagellare (Hedw.) Loeske	n=12		Crum, 1973
	n=23	Quebec	Anderson & Crum, 1958

(Continued)

TABLE 2. (Continued)

SPECIES	CHROMOSOME NUMBER	SOURCE LOCALITY	REFERENCE
Orthodicranum montanum (Hedw.) Loeske	n=12		Crum, 1973
	n=14		Crum, 1973
Orthodicranum strictum Culmann	n=14 (12+2)	Alberta	Anderson & Crum, 1958
	n=14	Washington	Ireland, 1967

Habitats of North American Dicrana and Orthodicrana

Dicranum is one of the most common genera of mosses found in the boreal region of the Northern Hemisphere, exceeded in cover only by *Sphagnum* spp., *Hylocommum splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., and possibly *Tomenthypnum nitens* (Hedw.) Loeske, *Aulacomnium palustre* (Hedw.) Schwaegr., and *Mnium* spp. (*sensu lato*) (La Roi and Stringer, 1976). Species of *Dicranum* and *Orthodicranum* occur in a wide variety of habits (Table 3) ranging from peatlands and mesic forests to sandy soils and decaying logs. Humus is the most common habitat with seven species occurring primarily in it. *D. majus* and *D. ontariense* are oceanic and suboceanic species respectively, with *D. majus* on both coasts and *D. ontariense* on the east coast and along the St. Lawrence River. *Dicranum polysetum* is a continental species commonly found in boreal forests on well drained humus; while three species, *D. pallidisetum*, *D. rhabdocarpum*, and *D. muchlenbeckii* are montane species. *D. pallidisetum* is restricted primarily to southern British Columbia and the state of Washington while *D. rhabdocarpum* is endemic to the Rocky Mountains, south of Wyoming. *D. muehlenbeckii* is also predominately found in the Rocky Mountains, but it ranges north into the Arctic. *D. scoparium*, the remaining moss occurring primarily on humus is the most cosmopolitan species of the genus, being found in all but the driest areas of North America. It is occasionaly found on decaying wood, mineral soil, soil over rocks, and more rarely in peatlands and arctic-alpine localities.

TABLE 3. Primary and secondary habitats of species of *Dicranum* and *Orthodicranum* that occur in North America.

	Tundra	Peatlands	Humus	Sand	Decaying Wood	Living Trees	Rocks	Mineral Soil
Orthodicranum flagellare			X		XX			
O. fulvum							XX	X
O. montanum					XX			
O. strictum					XX	X		
O. viride						XX		
Dicranum acutifolium	XX		X					
D. angustum	XX	X	X					
D. amannii	XX		X					
D. brevifolium v. *brevifolium*			X					XX
D. brevifolium v. *bistratosum*			X					XX
D. condensatum				XX				X
D. elongatum	XX		X					X
D. fragilifolium					XX			
D. fuscescens			X		XX			
D. groenlandicum	XX		X					
D. leioneuron		XX						
D. majus			XX					
D. muehlenbeckii	X		XX					X
D. ontariense			XX		X			
D. pallidisetum			XX					
D. polysetum		X	XX					
D. rhabdocarpum			XX					
D. scoparium	X	X	XX		X			X
D. spadiceum	XX		X					X
D. spurium				XX				
D. sulcatum						XX		
D. undulatum		XX	X					

XX = Primary Habitat (most common)
X = Secondary Habitat(s) (occasional)

Species with primary habitats of arctic or arctic-alpine tundra are *D. acutifolium*, *D. angustum*, *D. amanii*, *D. elongatum*, *D. groenlandicum*, and *D. spadiceum*. *Dicranum elongatum* often forms extensive, well exposed hummocks and mats several meters in diameter. The remaining five species usually occur in smaller mats or tufts in more sheltered areas such as among rock outcrops and intermixed with vascular plants and other bryophytes. *Dicranum acutifolium*, although predominately a tundra species, also occurs in the forested regions of the Canadian Rocky Mountains with regularity.

Dicranum undulatum and *D. leioneuron* are the only species with peatlands as primary habitats with the former occurring throughout the boreal and subarctic regions in mixed mires growing on hummocks with other such mosses as *Aulacomnium palustre*, *Tomenthypnum nitens*, and *Sphagnum fuscum*. In contrast, *D. leioneuron* occurs in ombrotrophic microhabitats and is restricted, in North America, to the Canadian Maritime provinces. *Dicranum condensatum*, a North American endemic, and its wider ranging relative, *D. spurium*, occur primarily on sandy soil in the southeastern portion of the United States. They are the only species to occupy this habitat, although one other species, *D. brevifolium* and its variety *bistratosum* are found primarily on mineral soil in rocky areas.

Wood, in various states of decomposition, accounts for primary habitats of three *Dicranum* species and four of the five *Orthodicranum* species. *Dicranum fuscescens*, *D. fragilifolium*, *O. flagellare*, and *O. montanum* commonly occur on angiosperm stumps or logs in various states of decay while *O. strictum* is more commonly found on coniferous logs. Two species, *D. sulcatum* and *O. viride* are usually found on living trees with the former on conifers of the west coast and the latter on angiosperms of eastern North America. The range of *O. viride* is quite similar to that of its close relative, *O. fulvum*; however, this last species is found on silicious rock and is the only species in either *Dicranum* or *Orthodicranum* to grow directly on rock.

TAXONOMIC TREATMENT

After studying over 12,000 specimens of *Dicranum* and *Orthodicranum* from all geographic areas of North, America, except Mexico, I believe both are justified generic status. I have subdivided *Dicranum* into five sections with twenty-one species, while *Orthodicranum* is composed of five species. Although a number of varieties have been described, only one is recognized in this revision.

Every effort was made to obtain type specimens. In the cases where type specimens were not examined, substantial material from the original authority's (or his colleague's) herbarium was seen in order to ascertain his concept of the species in question. Before the nomenclature code existed, holotypes were not designated by early bryologists and collections were often subdivided and distributed to several herberia. This practice resulted in isotypes in cases where one collection was designated in the description, and isosyntypes when more than one collection was designated. I have chosen a number of these as lectotypes (when a specimen from the original authority's herbarium was available), and the remainder have been noted as isotypes, syntypes or isosyntypes (as applicable). Holotype were only designated when a single specimen was cited by the author.

All drawings were made by myself with either a drawing tube or, in the case of capsules, from photographs. The distribution maps were plotted from specimens received on loan from numerous herbaria (Table 4) and from my own collections. In a few cases, reports of easily distinguished taxa were plotted as open circles; however, this was only done for geographic areas from which few specimens were seen such as Arctic Alaska (Steere, 1978), the Canadian Archipelago (Brassard, 1967, 1971; Brassard and Steere, 1968), and Newfoundland (Tuomikoski *et al.*, 1973). Geographic ranges outside North America were obtained from literature. The Goode Base Map series No. 2 and No. 101M are used with permission.

There are twenty-one species of *Dicranum* and five species of *Orthodicranum* indigenous to North America, many of which are difficult to identify, and this combined with the relative abundance of the species often leads to chaos as many specimens are collected and then misidentified. I have seen as many as seven different species filed in major herbaria under the name of *D. fuscescens* while such species as *D muehlenbeckii* and *D. pallidisetum* were ignored. With the lack of recent taxonomic consideration of species within *Dicranum*, and the increase in the use of *Dicranum* samples in ecological and physiological studies, I believe it is essential that the genus and its species be re-evaluated. Physiological or ecological studies are not of much use for comparative analysis if workers cannot correctly identify their experimental samples. It is the purpose of this thesis to examine *Dicranum* in North America and establish or confirm species concepts and geographical distribution patterns, as well as provide a workable key suitable to taxonomists and non-taxonomists alike.

TABLE 4. Herbaria from which specimens of *Dicranum* and *Orthodicranum* were examined. (Abbreviations from Iwatsuki *et al.*, 1976)

Official Abbreviation	Location
ALA	Fairbanks, Alaska, U.S.A.
ALTA	Edmonton, Alberta, Canada
ARIZ	Tucson, Arizona, U.S.A.
B	Berlin, Fed. Rep. of Germany
BM	London, Great Britain
C	Copenhagen, Denmark
CANM	Ottawa, Ontario, Canada
CAS	San Francisco, U.S.A.
COLO	Boulder, Colorado, U.S.A.
DUKE	Durham, North Carolina, U.S.A.
F	Chicago, Illinois, U.S.A.
FH	Cambridge, Massachusetts, U.S.A.
G	Genevé, Switzerland
H	Helsinki, Finland
HSC	Arcata, California, U.S.A.
L	Leiden, Netherlands
LAF	Lafayette, Louisiana, U.S.A.
MICH	Ann Arbor, Michigan, U.S.A.
MIN	Saint Paul, Minnesota, U.S.A.
MNA	Flagstaff, Arizona, U.S.A.
NFLD	Saint John's, Newfoundland, Canada
NY	New York, New York, U.S.A.
O	Oslo, Norway
PAC	University Park, Pennsylvania, U.S.A.
S	Stockholm, Sweden
SMS	Springfield, Missouri, U.S.A.

(Continued)

TABLE 4. (Continued)

Official Abbreviation	Location
SMU	Dallas, Texas, U.S.A.
TENN	Knoxville, Tennessee, U.S.A.
U	Utrecht, Netherlands
UAC	Calgary, Alberta, Canada
UBC	Vancouver, British Columbia, Canada
UC	Berkeley, California, U.S.A.
UPS	Uppsala, Sweden
US	Washington, D.C., U.S.A.
W	Wein, Austria
WTU	Seattle, Washington, U.S.A.
Z	Zürich, Switzerland

Morphology

Most *Dicranum* and *Orthodicranum* species produce sporophytes occasionally and, as a result, characters from both the sporophytic stage and the gametophytic stage have been used to delimit the taxa. The more important of these are individually discussed below.

Habit: Species of *Orthodicranum* and *Dicranum* grow as relatively unbranched, erect plants in populations varying from loose tufts where the individual plants are held together by tomentum and some intertwining, to dense mats where the plants are strongly matted by tomentum and much intertwining. The individual plants vary in height from less than one centimeter in *O. montanum* to greater than fifteen centimeters in *D. majus* and *D. polysetum*. Figures 5 through 12 show the basic habits of all species considered in this treatment. Points of importance include the curled appearance of *O. montanum* (Fig. 5-2), the broken yet somewhat falcate-secund leaves of *O. viride* (Fig. 5-4), the brush-like appearance and extremely straight capsules of *O. strictum* (Fig. 6-1) as opposed to the curved capsules and larger size of *D. fragilifolium* (Fig. 6-2). *Dicranum groenlandicum* (Fig. 8-3) and *D. undulatum* (Fig. 10-1) often have leaves appressed to the stem while *D. spurium* (Fig. 9-2) has leaves that arch away from the stem, and *Dicranum polysetum* (Fig. 10-3) and *D. majus* (Fig. 10-4) are polysetous with the former having obviously undulate leaves. *Dicranum angustum* (Fig. 10-1), *D. leioneuron* (Fig. 12-2), and *D. amannii* (Fig.

12-4) are quite similar in habit to the various forms of *D. scoparium* (Figs. 11-1, 11-2, 11-3, 11-4, 12-1). The attenuated branch tips of *D. leioneuron* (Fig. 12-2) are much more delicate than those found in forms of *D. scoparium* (Fig. 12-1).

Leaves: The leaves in *Dicranum* and *Orthodicranum* are radially arranged and may be erect and appressed as in *D. elongatum*, *D. groenlandicum*, and *D. undulatum*, falcate-secund as in *D. majus*, *D. fuscescens*, and *O. fulvum*, or contorted to crisped as in *D. brevifolium*, *D. condensatum*, and *O. montanum*. The leaf shape is usually lanceolate, ranging from narrowly lanceolate (Fig. 43-1) to broadly lanceolate (Fig. 61-1), and rarely, the leaves may be ovate-lanceolate (Fig. 37-1) or ovate (Fig. 51-3). The leaf apex is usually acute (Fig. 34-2) but may be rounded (Fig. 57-3) in a few cases, and often cucullate in *D. amannii* (Fig. 74-1).

Leaf cells: The cells are smooth in most species; however, papillae may be found on the abaxial laminal surface of such species as *D. fuscescens* (Fig. 27-12), *D. sulcatum* (Fig. 29-13), *D. condensatum* (Fig. 48-12), *D. spurium* (Fig. 51-13), and *D. ontariense* (Fig. 55-13). Several other species have papillae restricted to the abaxial costal surface (Figs. 19-13, 32-12). In one species, *D. brevifolium*, the papillae are not formed over the cell lumens as in the previous cases; they are the result of a protrusion of the cell walls between adjacent cells (Fig. 39-13). Areolation and shape of the laminal cells are extremely important taxonomic characters with the latter being the major criterion used to separate the section *Dicranum*, where the length/width ratio of the upper cells is greater than four to one, from the rest of the genus. The "upper cells" are not the cells of the extreme tip as these cells are often somewhat distorted and taxonomically unreliable. The "upper cells" are those found about twenty cells from the tip or, in the species where the costa is excurrent, about fifteen or twenty cells from the upper extreme of the lamina. In all *Orthodicranum* species and the majority of the remaining *Dicranum* species (Sections *Spuria*, *Elongata*, *Fuscescentiformia*, and *Muehlenbeckia*), the upper cells have a length/width ratio of less than three to one (Figs. 19-7, 25-6, 34-6). The median cells are similar in shape to the upper cells (except for *D. elongatum* where the upper cells are short (Fig. 43-6) and the median cells are elongate (Fig. 43-7)) and may be long and smooth (Fig. 59-7) or long and pitted (Fig. 61-7). When the median cells are shorter than four to one, they may be quadrate (Fig. 27-7) or rectangular (Fig. 23-7) or irregular in shape (Fig. 48-7). The areolation of the median leaf area may consist of cells in relatively straight rows (Fig. 27-7) or loosely arranged to the point where rows are difficult to determine (Fig. 53-8). The basal cells are usually long-rectangular, may or may not be pitted, and do not vary much in the genus. The alar region consists of enlarged, darkly coloured, more or less inflated cells that are a single layer thick in the genus *Orthodicranum* (Fig. 17-12) and two layers thick in the genus *Dicranum* (Fig. 48-13, 72-12). In addition, they normally have a few long-rectangular basal cells between them and the costa. In the few species where the inflated alar region does extend to the costa (Fig. 11-1), it is significant.

Transverse-section: Several important characters essential in distinguishing externally similar species are seen in a median transverse-section of the leaves. All *Dicranum* and *Orthodicranum* species have a single row of enlarged, centrally arranged guide cells (Fig. 15-14) except for *D. majus*, which differs diagnostically, with two rows (Fig. 63-13). Adjacent to both sides of the guide cells are bundles of thick-walled fiber-like cells that are termed stereids (Fig. 29-13), and these are present in all but *D. pallidisetum* (Fig. 32-12) and *O. strictum* (Fig. 23-12). In both cases, the absence of stereids assists in separating these species from others. In addition, stereids may have thick walls with small lumens (much more narrow than the thickness of the cell walls (Fig. 13-1)), or moderately developed with larger lumens (about the same diameter as the thickness of walls (Fig. 13-3)). The latter state is characteristic of *D. muehlenbeckii*, *D. spadiceum*, and *D. brevifolium*. In some cases, the stereids extend from the guide cells to both surfaces of the costa (Fig. 15-14) or occasionally the abaxial layer will be differentiated from the typical stereids by larger lumens (Fig. 29-13). Rarely, both the abaxial and adaxial layers will be differentiated in this manner (Fig. 34-12). This differentiation is taken to the extreme in the section *Dicranum* with the development of wing-like ribbons of tissue, termed lamellae, that extend from the abaxial surface of the costa (Fig. 68). They are also easily seen by examining the surface of the leaf with a lens. The transverse-section is also necessary to determine the number of laminal layers in the upper portion of the leaf. *Orthodicranum viride* (Fig. 21-12) and *D. brevifolium* var. *bistratosum* (Fig. 41-12) have almost entirely bistratose upper laminae, while *D. brevifolium* var. *brevifolium* (Fig. 39-12) and *D. majus* (Fig. 63-12) may have more restricted bistratose areas. Additional species that have bistratose margins and unistratose laminae include *D. fuscescens* (Fig. 27-13), *D. sulcatum* (Fig. 29-12), *D. pallidisetum* (Fig. 32-13), *D. acutifolium*, and *D. ontariense*.

Asexual reproductive structures: Specialized asexual reproductive structures are of three types in *Orthodicranum* and *Dicranum*, 1) fragile leaf tips (Figs. 19-3, 23-2, 25-2), 2) flagellated branches (Fig. 5-1), and 3) attenuated stem tips (Figs. 12-1, 12-2). The fragile leaf tips are produced by *O. strictum*, *O. viride*, and *D. fragilifolium* and easily broken off by the slightest pressure. All of these species normally grow in sheltered forests on logs and stumps and consequently it is easy to imagine numerous small animals brushing against the plants and fracturing the leaves. The broken tips are often up to 2 mm in length and therefore, they are probably not dispersed over great distances. Nevertheless, they are very effective at reproducing the species at short distances. The flagellated branches of *O. flagellare* act in a similar fashion. The branches often segment into several sections, each of which is capable of producing a new colony. The attenuated branch tips of *D. scoparium* and *D. leioneuron* do not seem to be as efficient as the other structures. They are little more than slightly reduced stem leaves that protrude above the colony. They are not easily broken off nor are they small enough to be dispersed very far when they are broken off.

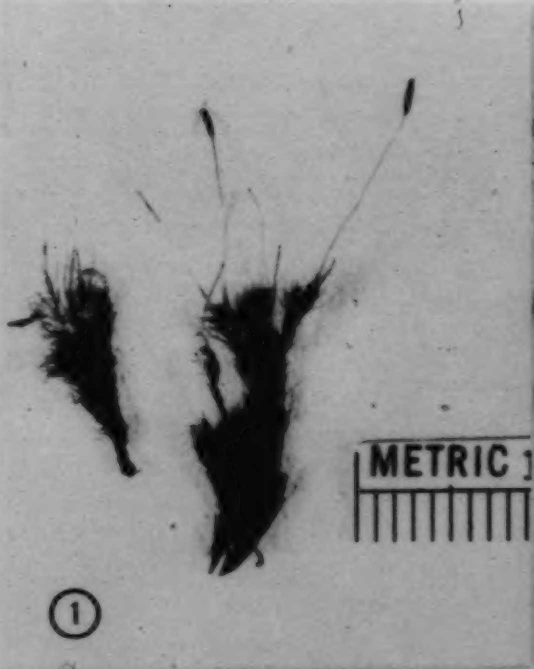
Sporophyte: Species of *Dicranum* and *Orthodicranum* have setae ranging from about 0.5 cm to about 4.5 cm in length and occur one per perichaetium (monosetous) except for three species of *Dicranum* (*D. majus*, *D. ontariense*, and *D. polysetum*) which have two to five setae per perichaetium (polysetous). The capsules are straight in *Orthodicranum* (Figs. 15-11, 19-11) and curved in most *Dicranum* species (Figs. 27-10, 29-9). When curved, they may be strumose (Fig. 27-10) or not (Fig. 61-9), and the neck may be short (Fig. 48-10) or long (Fig. 34-10).

The opercula of both *Orthodicranum* and *Dicranum* are conic in shape, with a long rostrum that may be either straight (Fig. 19-10) or curved (Fig. 63-10). The surface is smooth. The peristome consists of 16, forked, vertically striate teeth with little variation among the species. Occasionally the teeth may be cribbose (Fig. 70-10) or have a slight basal membrane (Fig. 41-11). The teeth of *Orthodicranum* species are generally more narrow (<60 μm wide) than those of *Dicranum* (>70 μm wide). The presence or absence of an annulus is significant in both genera. *Orthodicranum strictum* and all members of *Dicranum* section *Dicranum*, except *D. angustum*, are without this structure. The remaining species have an annulus composed of one to three rows (variable in all species) of very thick-walled, hyaline cells which, upon separation of the opercula, normally fragment into numerous sections. The calyptrae of all *Dicranum* and *Orthodicranum* species is cucullate and smooth.

5.

FIGURE 5. Growth Habits

1. *Orthodicranum flagellare* (Hedw.) Loeske
2. *O. montanum* (Hedw.) Loeske
3. *O. fulvum* (Hook.) Roth.
4. *O. viride* (Sull.) Roth.



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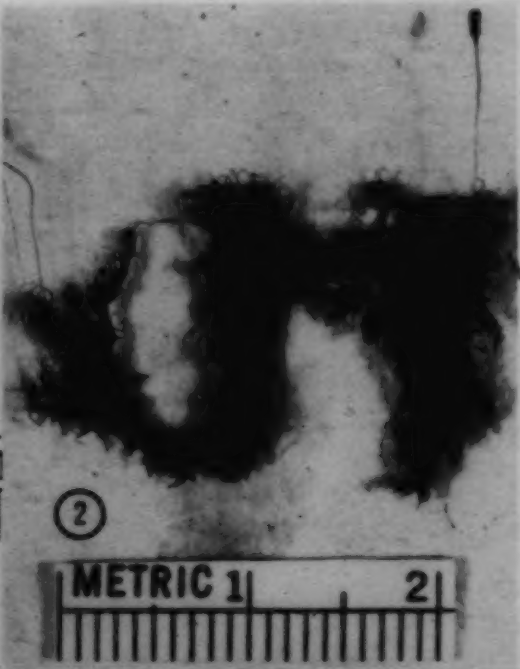

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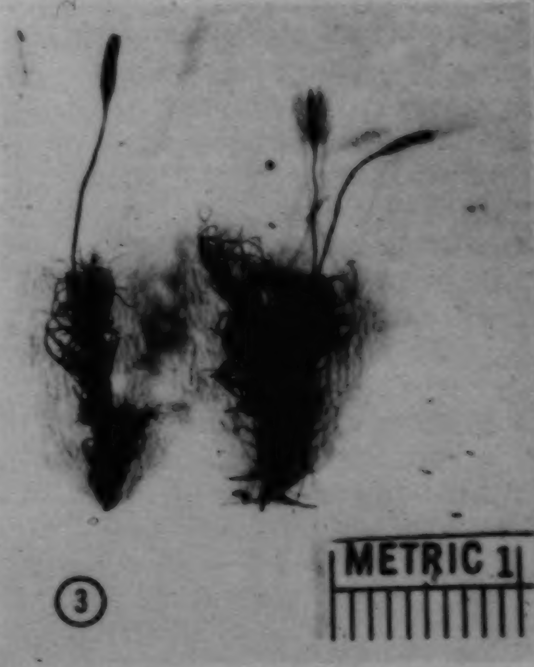

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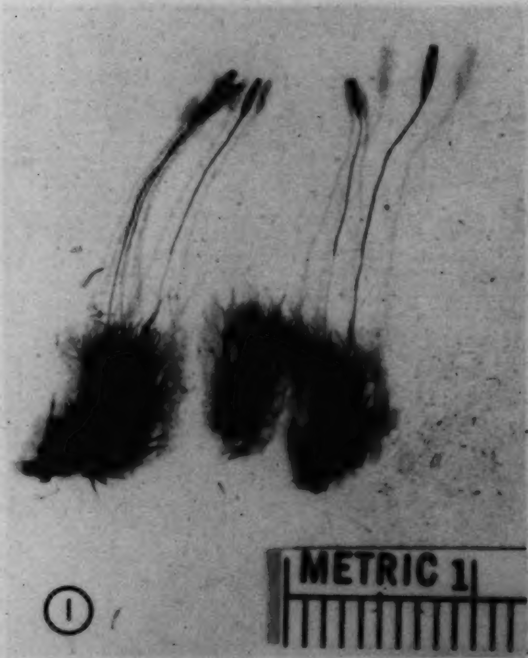
FIGURE 6. Growth Habits

1. *Orthodicranum strictum* Culmann
2. *Dicranum fragilifolium* Lindb.
3. *D. fuscescens* Turn.
4. *D. sulcatum* Kindb.



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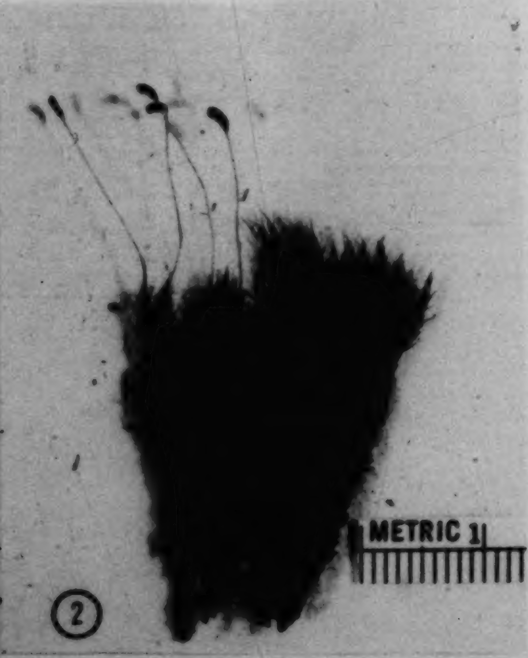

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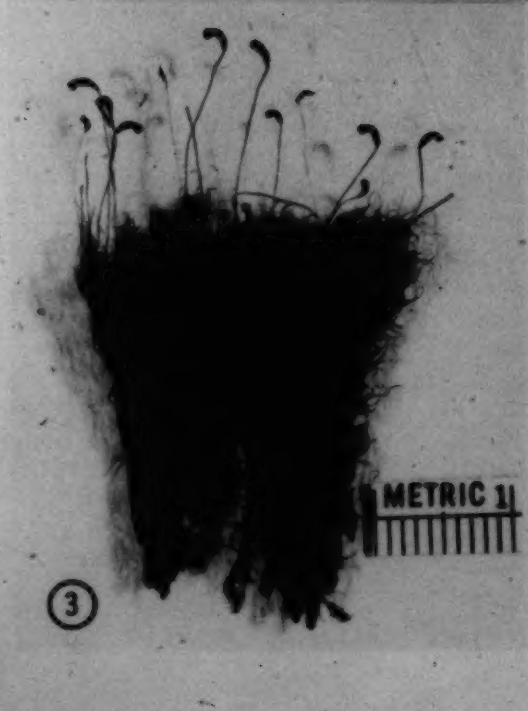

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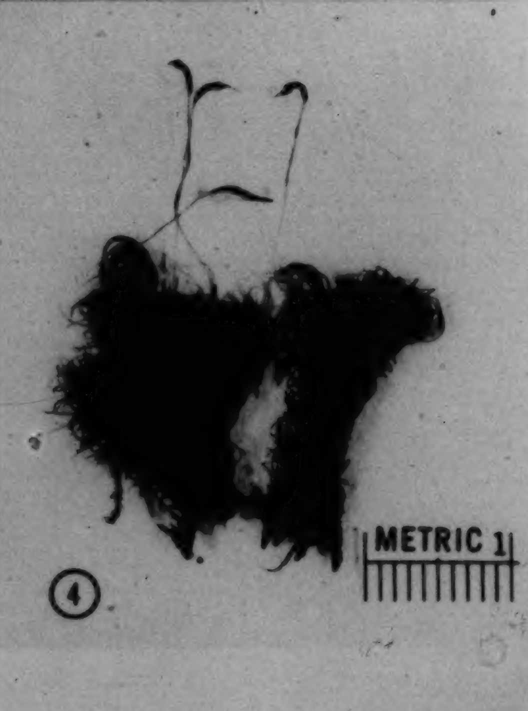

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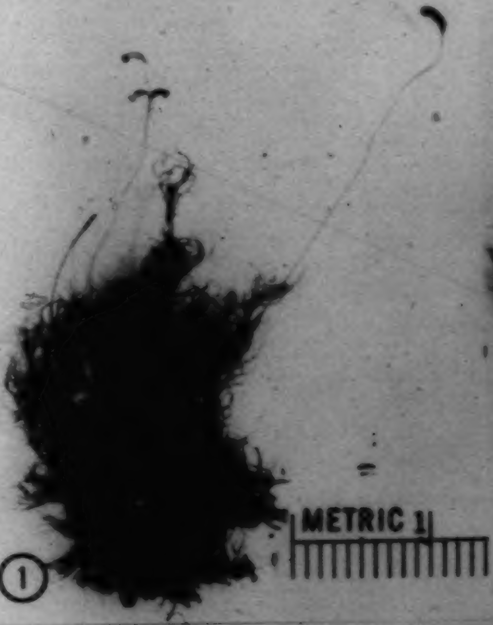
FIGURE 7. Growth Habits

1. *Dicranum pallidisetum* (Bailey) Ire.
2. *D. muehlenbeckii* B.S.G.
3. *D. spadiceum* Zett.
4. *D. brevifolium* Lindb. var. *brevifolium*



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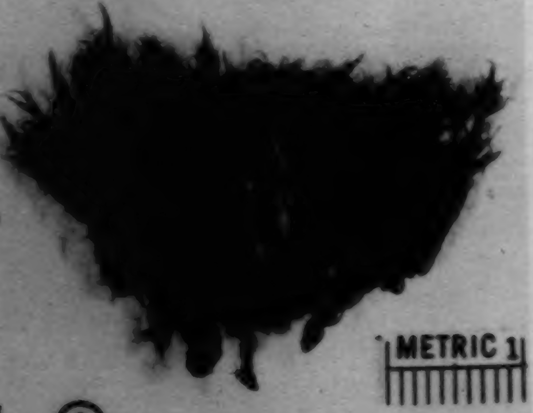

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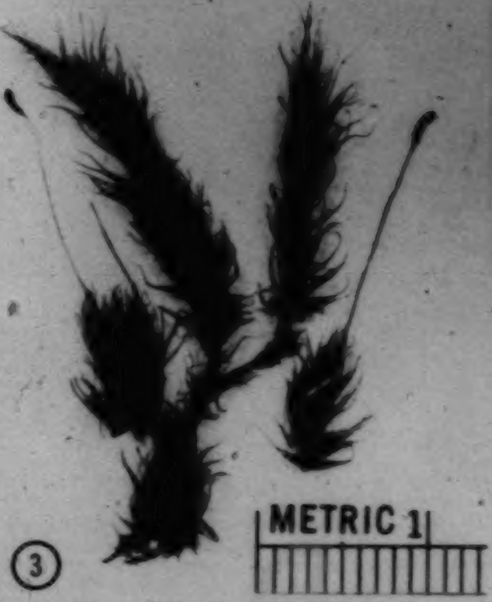

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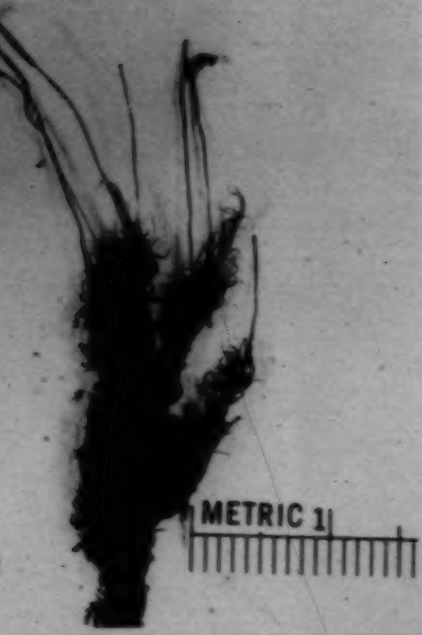

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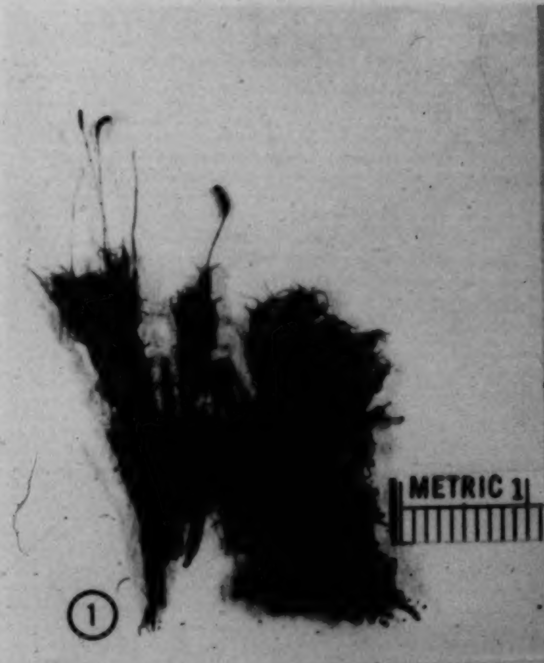
FIGURE 8. Growth Habits

1. *Dicranum brevifolium* var. *bistratosum* Peterson.
2. *D. elongatum* Schleich.
3. *D. groenlandicum* Brid.
4. *D. drummondii* C.M.



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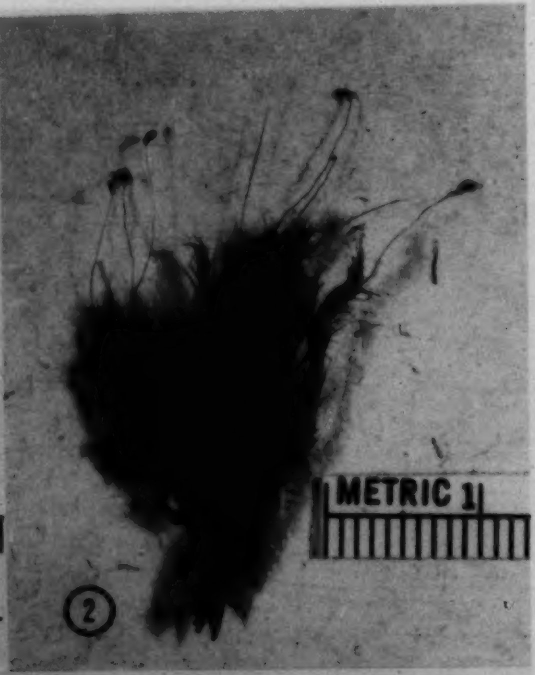

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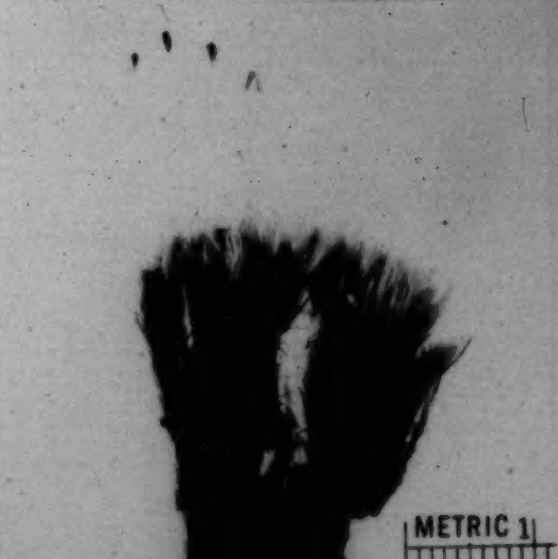

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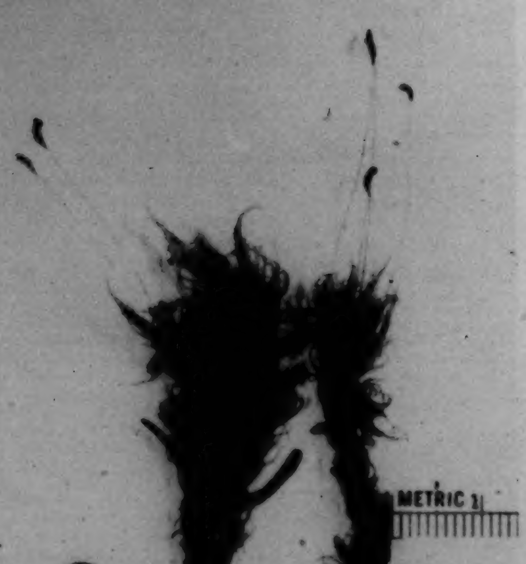

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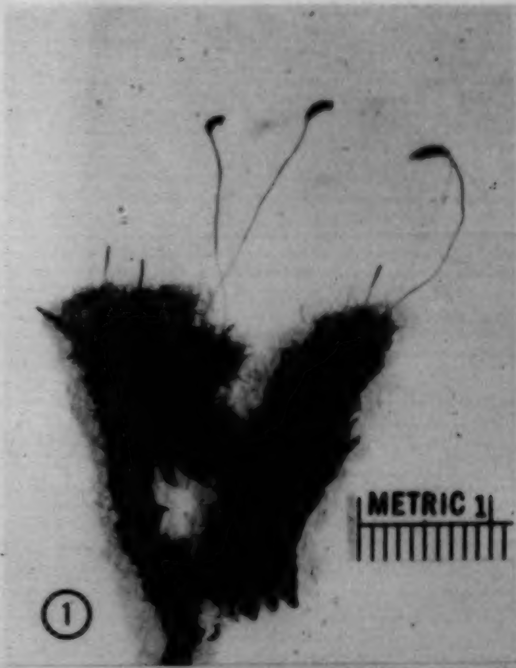
FIGURE 9. Growth Habits

1. *Dicranum condensatum* Hedw.
2. *D. spurium* Hedw.
3. *D. acutifolium* (Lindb. and Arn.) C. Jens.
4. *D. ontariense* Peterson



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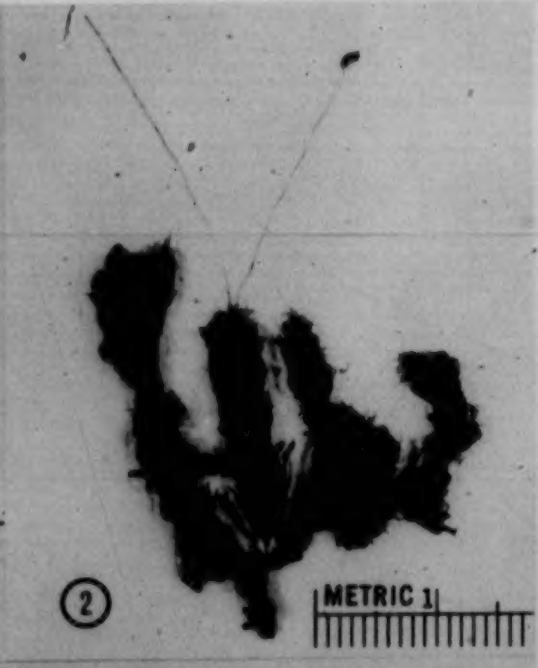

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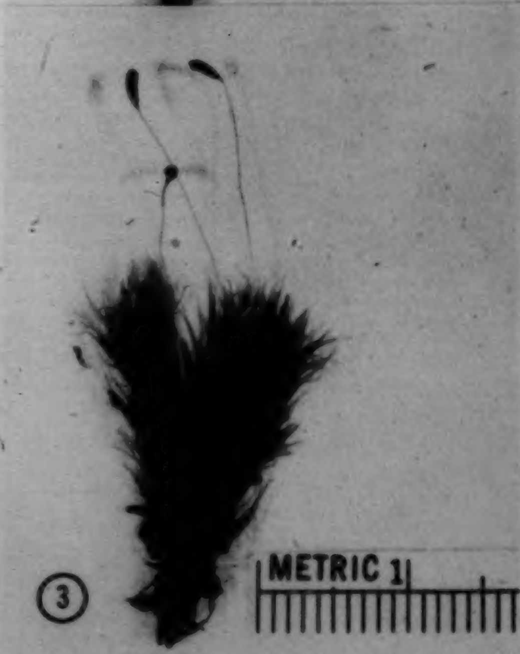

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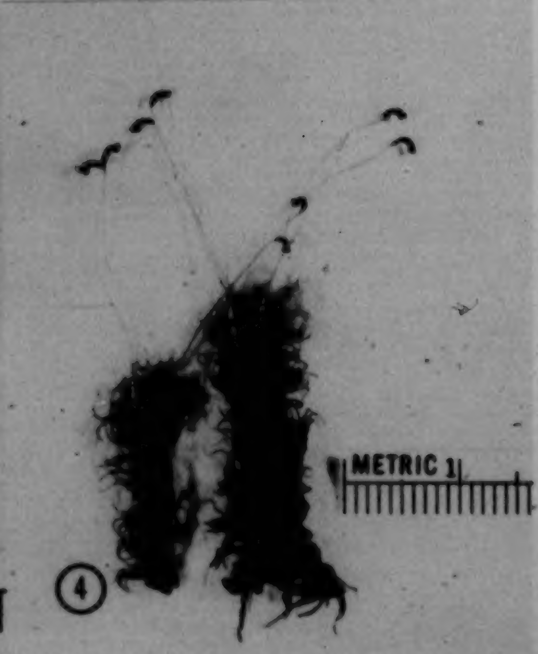

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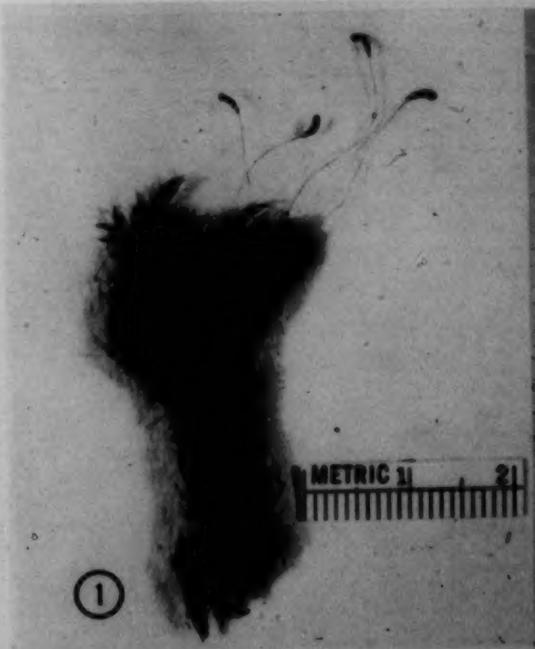
FIGURE 10. Growth Habits

1. *Dicranum undulatum* Brid.
2. *D. angustum* Lindb.
3. *D. polysetum* Sw.
4. *D. majus* Sm.



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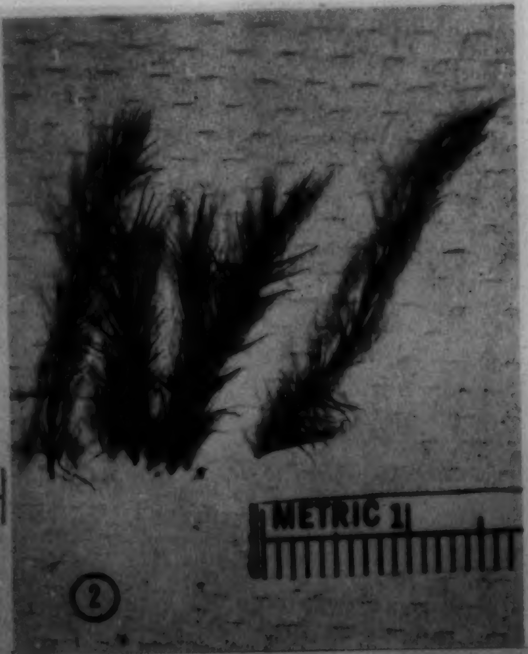

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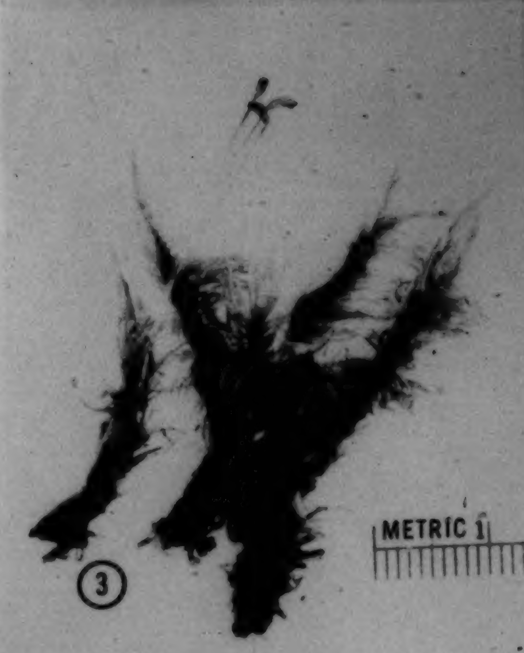

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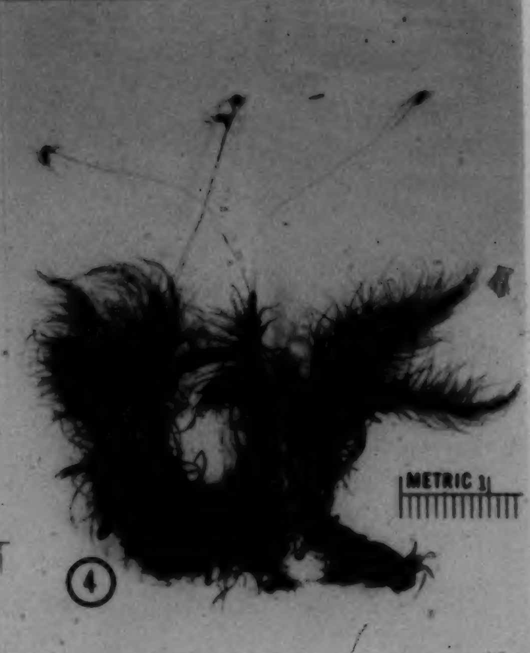

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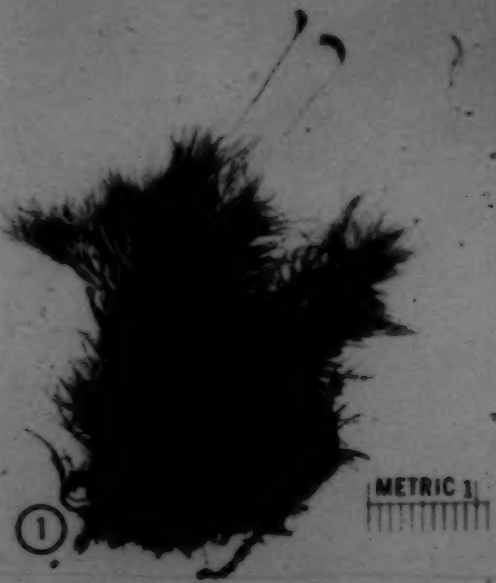
FIGURE 11. Growth Habits

1. *Dicranum scoparium* Hedw. (typical)
2. *D. scoparium* (a form)
3. *D. scoparium* (a form)
4. *D. scoparium* (a form)



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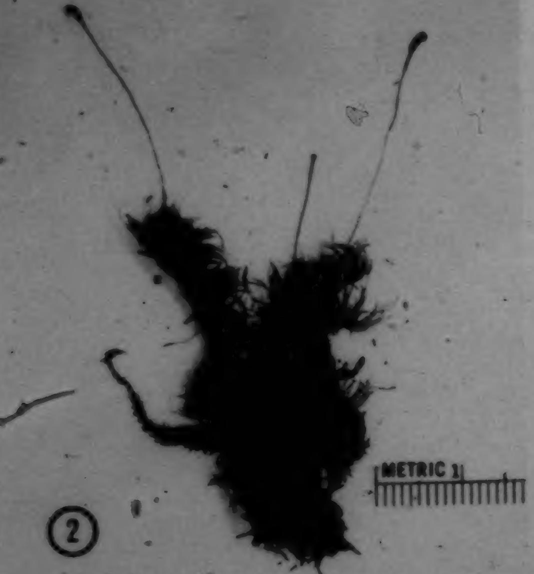

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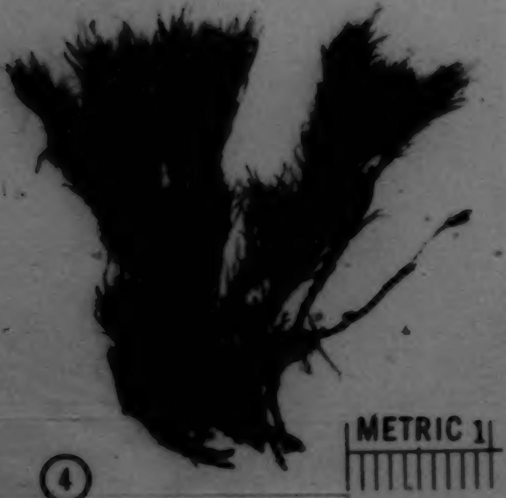

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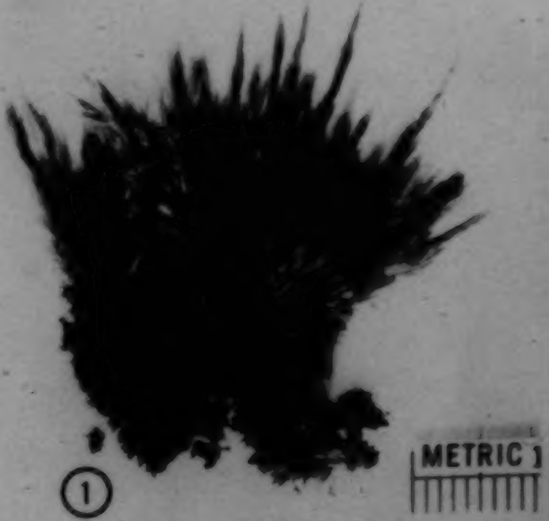
FIGURE 12. Growth Habits

1. *Dicranum scoparium* Hedw. (a form)
2. *D. leioneuron* Kindb.
3. *D. rhabdocarpum* Sull.
4. *D. amannii* Peterson



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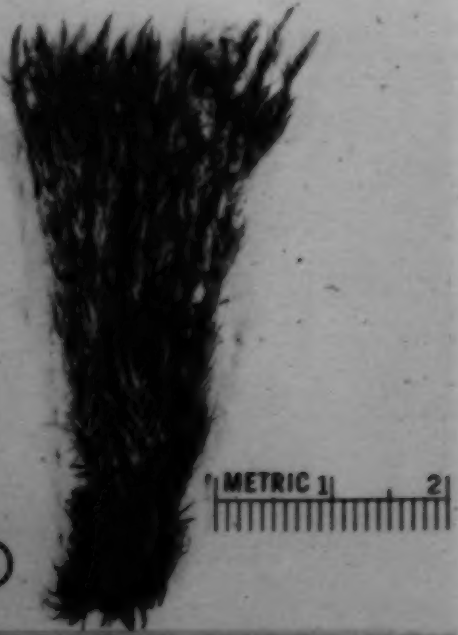

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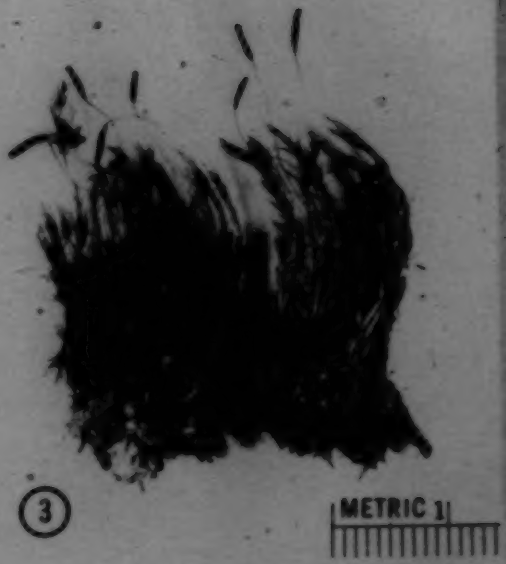

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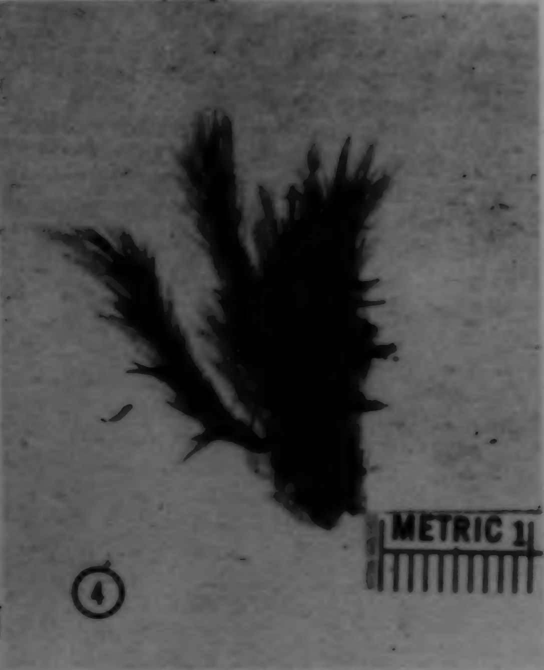

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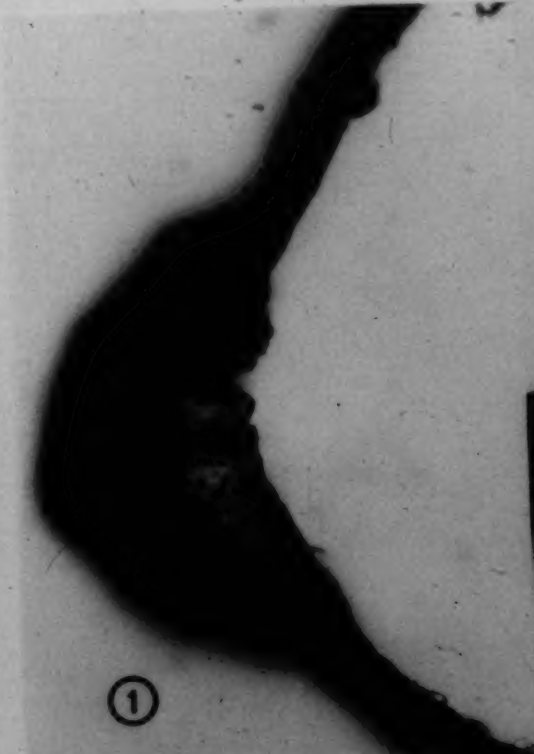
FIGURE 13. Transverse-sections of *Dicranum* costae showing the types of stereid and guide cells found in the genus.

1. *Dicranum sulcatum* Kindb. with small stereid lumens and one row of guide cells.
2. *Dicranum scoparium* Hedw. with small stereid lumens and four lamallae projecting from abaxial surface.
3. *Dicranum brevifolium* Lindb. with lumens of the stereids about as wide as the thickness of the walls.
4. *Dicranum majus* Sm. with a double row of guide cells.



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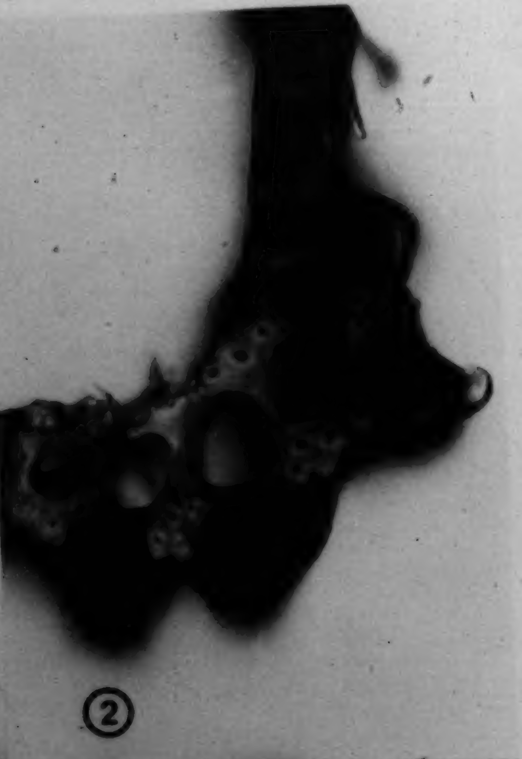

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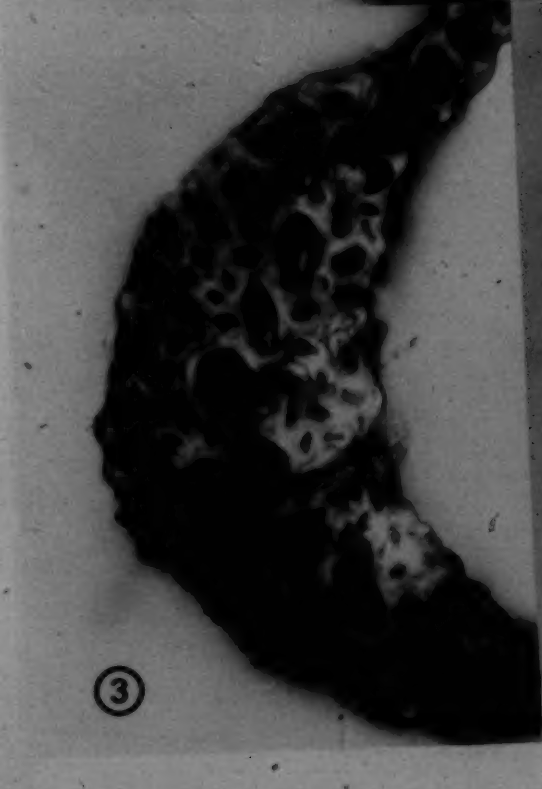

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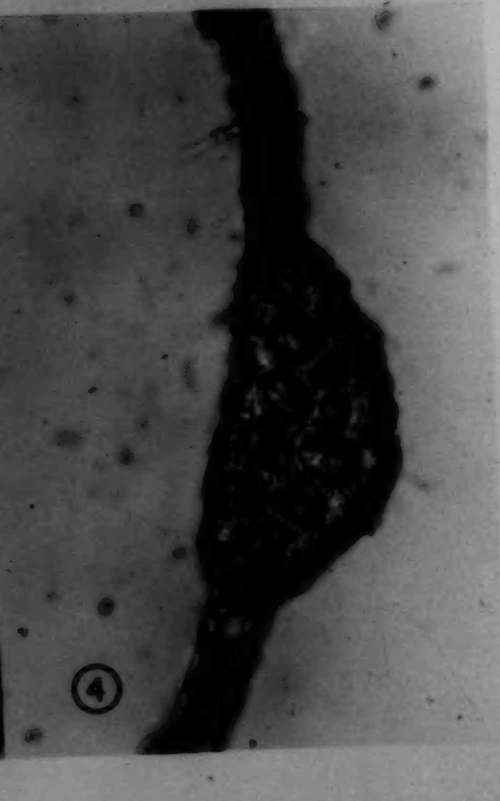

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A Key to North American
Dicranum and *Orthodicranum*

1. Leaf tips broken, leaves straight and stiff 2

1. Leaf tips intact, leaves falcate-secund, crisped, or rarely straight 4

    2. Capsules curved, alar cells bistratose and usually extending to the costa .. *Dicranum fragilifolium* (#6)

    2. Capsules more or less erect, alar cells unistratose and not extending to costa 3

3. Stereid cells present only in base of costa; costa narrow (1/6 to 1/5 width of leaf base); specimens growing on wood west of Rocky Mountains .... *Orthodicranum strictum* (#5)

3. Stereid cells present throughout costa; costa wide (1/4 to 1/3 width of leaf base); specimens growing on trees in eastern North America .... *O. viride* (#4)

    4. Flagellated branches present in upper leaf axils; capsules erect; specimens usually found growing on wood .... *O. flagellare* (#1)

    4. Flagellated branches absent, or if present, capsules curved; specimens found growing on wood, humus or soil 5

5. Leaves transversely undulate 6

5. Leaves without transverse undulations 13

    6. Majority of cells in upper part of lamina elongate (>4:1) and strongly pitted (Figs. 61-6, 65-6); plants generally robust (3 to 15 cm tall) 7

    6. Majority of cells in upper part of lamina short (<3:1) with smooth or slightly pitted cells walls (Figs. 17-6, 27-6); plants generally small (1 to 6 cm tall) 9

7. Plants polysetous; lacking filiform branches; leaves spreading and strongly serrate in upper 1/2 or more .... *D. polysetum* (#21)

7. Plants monosetous; filiform branches often present; leaves imbricate or falcate-secund and only slightly serrate in upper 1/3 or less 8

8. Stem leaves plainly undulate; attenuated stem tips, when present, with entire leaves; plants of ombrotrophic bogs in the Canadian Maritime Provinces ..... *D. leioneuron* (#24)

8. Stem leaves only slightly undulate; attenuated stem tips, when present, with serrate leaves; plants of minerotrophic areas in western North America and the Arctic .... *D. scoparium* (#23)

9. Many median cells wider than long; capsules strumose and attached to setae at about a 90° angle (Fig. 48-10) 10

9. Most median cells longer than wide; capsules not strumose, attached to seta at angles greater than 90° (Figs. 53-11, 55-9) 11

10. Leaves broadest near the middle, diverging from stem at a wide angle (*ca.* 90°); lamina densely papillose on abaxial surface .... *D. spurium* (#16)

10. Leaves broadest near the base, diverging from stem at a lesser angle (*ca.* 45°); papillae generally restricted to abaxial surface of costa . *D. condensatum* (#15)

11. Leaf tip broad; costa sub-percurrent; plants of bogs and fens .... *D. undulatum* (#19)

11. Leaf tip acute to narrowly acute; costa percurrent to excurrent; plants of forests or on soil in alpine communities 12

12. Polysetous; plants robust (5 to 10 cm tall); abaxial surface of costa and lamina papillose .... *D. ontariense* (#18)

12. Monosetous; plants smaller (<4 cm tall); papillae restricted to abaxial surface of costa .... *D. acutifolium* (#17)

13. Majority of cells in upper part of lamina elongate (>4:1) and strongly pitted (Fig. 61-6) 14

13. Majority of cells in upper part of lamina short (<3:1) with smooth or slightly pitted walls (Figs. 15-8, 39-6) 20

  14. Capsules erect to semi-erect (Figs. 15-11, 46-10, 72-9) 15

  14. Capsules plainly curved (Figs. 48-10, 59-9, 61-10) 16

15. Laminal cells very thick-walled (Fig. 46-6); plants growing in thick tufts, usually arctic-alpine .... *D. groenlandicum* (#14)

15. Laminal cells thin-walled (Fig. 72-6); plants growing in loose mats, in montane regions of the Rocky Mountains south of Wyoming ..... *D. rhabdocarpum* (#25)

  16. Polysetous; guide cells as seen in median transverse-section consisting of two rows (Fig. 63-13) .... *D. majus* (#22)

  16. Monosetous; guide cells as seen in median transverse-section consisting of one row 17

17. Costa, as seen in median transection-section, with only 3 or 4 guide cells and without stereid bands; monoicous .. *Kiaeria glacialis* (not treated)

17. Costa, as seen in median transverse-section, with 4 to 6 guide cells and two stereid bands; dioicous 18

  18. Leaves in median transverse-section showing lamellae or at least enlarged cells along the abaxial surface of the costa .... *D. scoparium* (#23)

  18. Leaves in median transverse-section without lamallae 19

19. Leaves wide (Fig. 74-1); leaf tip usually concave or cucullate; alar cells thick-walled .. *D. amannii* (#26)

19. Leaves narrow; leaf tip acute, not concave or cucullate; alar cells thin-walled .... *D. angustum* (#20)

20. Capsules erect; alar region unistratose; plants small (usually <1 cm tall) and usually found growing on wood or rock 21

20. Capsules curved; alar region bistratose; plants medium to large (>2 cm tall); found growing on soil or humus or occasionally on wood 23

21. Plants usually growing on rock, costa wide (1/3 to 1/4 width of leaf base); basal cells short and similar to median cells .... *O. fulvum* (#3)

21. Plants usually growing on wood; costa about 1/6 width of leaf base; basal cells elongate 22

22. Leaves strongly crisped; leaf cells in transverse-section showing slightly bulging walls and some papillae; plants usually <0.5 cm tall .... *O. montanum* (#2)

22. Leaves slightly crisped to falcate-secund; leaf cells in transverse-section smooth; plants up to 3 cm tall .... *O. flagellare* (#1)

23. Leaves tubulose (costa not a prominent ridge on abaxial leaf surface) 24

23. Leaves keeled (costa prominent as a ridge or fold on abaxial leaf surface 27

24. Costa in median transverse-section lacking bands of stereid cells (Fig. 32-12) .... *D. pallidisetum* (#9)

24. Costa in median transverse-section with two well-developed bands of stereid cells 25

25. Alar cells unistratose; plants small (1 to 3 cm tall) usually growing on wood .... *O. flagellare* (#1)

25. Alar cells bistratose; plants medium to large (>3 cm tall); usually found growing on soil or humus 26

26. Both adaxial and abaxial rows of external costal cells differentiated from stereid cells by large lumens; costa 100 to 120 μm wide near leaf base; spores <20 μm .... *D. muehlenbeckii* (#10)

26. Only abaxial row of external costal cells differentiated from stereid cells by large lumens; costa 65 to 80 μm wide near leaf base; spores >20 μm .... *D. spadiceum* (#11)

  27. Upper cells rounded, with very thick walls (Fig. 43-6); leaves usually straight, imbricate; plants usually found growing in compact tufts in arctic or alpine regions .... *D. elongatum* (#13)

  27. Upper cells quadrate (Fig. 27-6) or variously angled (Fig. 57-7) or slightly rounded, with thin walls (Fig. 41-6); leaves falcate-secund or slightly spreading; usually found growing in loose mats or tufts in montane or rarely in alpine areas 28

28. Median costal transverse-section showing strongly developed, small lumened, thick-walled stereids (Fig. 13-1); cell walls between laminal cells smooth 29

28. Median costal transverse-section showing moderately developed, large lumened, thin-walled stereids (Fig. 13-2); cell walls between laminal cells often protruding as papillae (Fig. 39-13) 31

  29. Median leaf cells in loose irregular rows; upper cells variously angled (Fig. 53-8) and with a few cells longer than wide (3 or 4:1) .... *D. acutifolium* (#17)

  29. Median leaf cells in rather regular vertical rows (Fig. 27-7); upper cells quadrate (Fig. 27-6) 30

30. Median costal transverse-section showing two stereid bands, each of about 4 rows of cells; papillae common on abaxial laminal and costal surface; costa distinctly long-excurrent ... *D. sulcatum* (#8)

30. Median costal transverse-section showing two stereid bands, each of about 2 rows of cells; papillae, if present, low and generally restricted to abaxial costal surface; costa percurrent or only slightly excurrent ..... *D. fuscescens* (#7)

31. Upper lamina unistratose; margins occasionally bistratose in spots .... *D. brevifolium* var. *brevifolium* (#12a)

31. Upper lamina bistratose or at least with numerous bistratose areas; margins bistratose or occasionally tristatose in spots ...... *D. brevifolium* var. *bistratosum* (12b)

Orthodicranum (C. Müll) Loeske, Stud. Morph. Syst. Laubm. 85: 1910.

Section: *Orthodicranum* C. Müll., Syn. 1: 371. 1848.
Lectotype: *Dicranum flagellare* Hedw.

Section: *Orthocarpa* B.S.G., Bryol. Eur. 1: 117. (Fasc. 37-40 Mon. 11). 1847.
Lectotype: *Dicranum flagellare* Hedw.

Subgenus: *Orthodicranum* (C. Müll.) B.S.G., Bryol. Eur. 1:6 (Fasc. 46-47 Consp. 1: VIII) 1851.

Scytalina Hagan, K. Norsk. Vid. Selsk. Skrift. 1914 (1): 129. 1915. *Nom. illeg. incl. gen. prior.*

Plants small, up to 3.5 cm tall, in dense mats or loose patches on decaying logs and occasionally on humus or rocks. Stems erect, sparsely branched, lightly tomentose. Leaves when dry falcate-secund to crisped, when moist straight to falcate-secund, lanceolate to narrow-lanceolate, occasionally with fragile leaf tips, smooth or papillose on abaxial surface, not undulate; lamina unistratose or occasionally bistratose near the apex; apex acute to long acuminate; margins plane, unistratose, entire or serrulate; costa narrow, 1/5 to 1/8 of leaf base width (wider in *O. fulvum* and *O. viride*), excurrent or percurrent, smooth or papillose on abaxial surface, in median transverse section showing 4 to 6 guide cells and two stereid bands (none in *O. strictum*), one abaxial and one adaxial to the guide cells and extending into the leaf apex, the adaxial and abaxial layer of external cells occasionally differentiated from stereids by larger lumens; lower laminal cells elongate, rectangular, thin-walled, sometimes slightly pitted, median cells rectangular or quadrate, seldom pitted, upper cells quadrate or short-rectangular, not much different from median cells; alar cells always present, unistratose, thin-walled, slightly inflated and dark-brown to dark-red, sometimes extending into the costa. Perigonia ovate, about 1.5 mm long, usually attached slightly below stem apex; antheridia club-shaped, 0.3 - 0.5 mm long, 8 to 12 per perigonium, intermixed with filamentous paraphyses. Archegonia slender, 0.5 - 0.7 mm long, 4 to 6 per perichaetium. Vegetative reproduction common by broken leaf tips or by flagellated branches (*O. flagellare*) borne in the axils of the upper stem leaves.

Dioicous, male plants growing intermixed with female or in separate mats. Perichaetial leaves usually shorter than stem leaves, abruptly acuminate to a subulate tip. Monosetous, setae extending well above leaves, yellow to brown. Capsules erect, cylindric, to 4 mm long, smooth or slightly wrinkled, never strumose, neck short; exothecial cells rectangular, thin-or thick-walled; stomates few, in one row at base of capsule; opercula conic with a short rostrum, smooth; peristome of 16 teeth inserted on capsule rim and divided about half way to the base into two forks, the outer surface vertically striate in the lower 1/2 or more, usually papillose above; annulus absent or consisting of 1 or 2 rows of enlarged, thick-walled hyaline cells, usually fragmenting; spores green to brown, 10-25 µm, papillose. Calyptrae cucullate and smooth.

Habitat: Specimens of *Orthodicranum* are most commonly found growing on wood, and depending upon the species, this may be living trees

(*O. viride*), conifer logs (*O. strictum*) or angiosperm logs (*O. montanum* and *O. flagellare*). *Orthodicranum fulvum* is the only member to be found predominately on rocks, although *O. montanum* occasionally occurs there. All five of the species may occasionally be found growing on other substrates such as humus, but this situation is exceptional.

Distribution: *Orthodicranum* is widespread in North America with species occurring in all regions where large forests are found. All but *O. strictum* are found in the eastern portion of North America and all are reported from Europe or portions of Asia. In North America, the most widespread species is *O. flagellare*, with specimens having been collected in all provinces of Canada and south as far as Mexico. *O. viride* has the most restricted distribution, occurring along the St. Lawrence River inland to Minnesota and southward in the Appalachian Mountains to Tennessee and North Carolina. No species of *Orthodicranum* occurs in the southern hemisphere.

Nomenclature: As to the correct authority for the name *Orthodicranum*, *Index Muscorum* (Wijk *et al.*, 1962) listed the genus as *Orthodicranum* (B.S.G.) Loeske, thus crediting Bruch, Schimper and Gümbel with the basionym for using the name at the subgeneric level in the conspectus of their 1851 publication. However, the name was first used by Carl Müller in 1848, who provided a description, at the section level and the correct authority citation for the genus is *Orthodicranum* (C. Müller) Loeske.

Taxonomy: As stated in the Introduction, *Orthodicranum* has not been widely accepted as a distinct genus by North American bryologists while European bryologists have usually considered it to be distinct at that level. The, as yet, marginal acceptance of the genus is probably due to the emphasis put upon the straight capsules after which the genus was named. I agree that this single character is not sufficient to separate a distinct genus, especially when it is found in species unquestionably in *Dicranum* (*D. groenlandicum*); however, no species of *Dicranum* except (*D. fragilifolium* which has broken leaf tips and grows on wood) has over one of the character states that I use to distinguish *Orthodicranum* (Table 1). Of these six characters, the erect capsule is still the most critical in defining the genus and the additional character states solidify it. The capsules in *Orthodicranum*, in addition to being straight, have only slightly wrinkled walls, and this usually occurs after the spores have been discharged. *Dicranum* species, including *D. groenlandicum*, have ribbed capsules. The other sporophytic character that is supportive to *Orthodicranum* is the narrowness of the peristome teeth. This is not a function of capsule size even though *Orthodicranum* species sometimes have capsules smaller than most *Dicranum* species. All *Orthodicranum* species commonly have capsules as large as those of many *Dicranum* species (2 — 4 mm long) and the peristome is always narrower (<60 µm) in *Orthodicranum*.

The gametophytic character states of unistratose alar regions and asexual reproduction, as well as the specialized habitats of wood and rock, also support the distinctness of *Orthodicranum*. Unistratose alar regions occur in all species of *Orthodicranum* and are rarely found even in the most depauperate specimens of *Dicranum* species. Normally *Dicranum* species will have at least one or two bistratose spots in the alar regions (Fig. 72-12) or will be entirely bistratose (Fig. 48-13). The asexual reproduction capabilities are by no means restricted to *Orthodicranum*, being found in *D. scoparium*, *D. leioneuron*, and *D. fragilifolium*; however, consistency is found only in the latter where broken leaf tips occur, while the former two species only occasionally have flagellated branches or attenuated stem tips. Most species of *Orthodicranum* consistently have broken leaf tips to some degree (*O. fulvum*, *O. strictum*, *O. viride*) or flagellated branches (*O. flagellare*). *Orthodicranum montanum* has neither broken leaf tips nor flagellated branches, but may have attenuated stem tips. Similarly, the habitat of wood or rock is not distinctive to *Orthodicranum* with three *Dicranum* species (Table 3) having wood as a primary habitat. It is the fact that no *Orthodicranum* species has a primary habitat other than wood or rock that is important.

Again, it is my opinion that the six characters are more than sufficient to solidify the validity of *Orthodicranum* at the generic level. It is true that sterile specimens may be confused with *Dicranum* and be difficult to identify but this does not mean the species themselves lack distinguishing characters.

1. *Orthodicranum flagellare* (Hedw.) Loeske, Stud. Morph. Syst. Laub. 85. 1910.

Dicranum flagellare Hedw., Spec. Musc. 130. 1801.

Type: *"Habit in truncis putridis prope Malchin Megapolitanum, in franconis."* (Lectotype-G!)

Dicranum miquelonense Ren. et Card., Bot. Gaz. 14: 98: 1880.

Type: "Miquelon Island, on ground and rocks." (Syntype - CANM!)

Dicranum miquelonense Ren. et Card. var. *crispatulum* Röll, Hedwigia 36: 1897.

Type: "Durham, New Jersey." (Isotype - NY!)

Dicranum crispatulum (Röll) Kindb., Eur. and N.Am. Bryin. (2) 189. 1897.

Scytalina flagellaris (Hedw.) Hagen, K. Norsk. Vid. Selsk. Skrift. 1914. (1) 132. 1915.

Plants small, up to 4 cm tall, in loose mats on decaying wood or humus, rarely on soil. Stems moderately tomentose, tomentum light-brown to dark-brown. Leaves when dry crisped and contorted, when moist falcate-secund to straight, not undulate, (2.0) 2.5-4.5 (5.0) mm long, lanceolate, tapering to an acute tip, tubulose in upper 1/3, slightly concave below, not keeled above or below, abaxial and adaxial surfaces smooth; margins entire or serrulate in upper 1/4, unistratose; costa narrow, 35-55 µm wide just above alar region, percurrent, rarely subpercurrent, toothed on upper abaxial surface, costa in median transverse-section showing 5 to 7 guide cells and 2 well developed stereid bands, both bands extending into upper 1/4 of leaf, each band composed of 2 to 3 cell layers, neither adaxial or abaxial layer of external cells differentiated from stereid cells; alar cells brown to red-brown, thin-walled, unistratose, not extending to the costa; basal cells above alar region rectangular, (20) 25-50 (65) µm long, thick-or thin-walled, walls smooth, not pitted; median cells (8) 10-14 (20) µm long, quadrate to short rectangular, thin-walled, walls smooth, not pitted, cells in fairly uniform rows; upper cells similar to median or slightly larger (8.0) 10-20 (25) µm long. Specialized flagelliform branches usually present in upper leaf axils, branches stiff, erect 2.0-5.0 (8.0) mm long, leaves of flagelliform branches short, lingulate, with broadly acute or obtuse apices, costa percurrent or subpercurrent, stereid bands absent, alar cells absent, laminal cells similar to median cells of stem leaves, branches often fragmenting into sections containing 1 to 4 leaves. Perichaetial leaves abruptly narrowed to a short subulate tip.

Dioicous, male plants similar to female ones. Monosetous, setae brown, (0.7) 1.0-2.5 cm long. Capsules light-brown to dark-brown, 2.0-3.5 (4.0) mm long, erect, cylindrical, slightly and irregularly wrinkled, constricted below the mouth, neck short; exothecial cells rectangular, angled, thick-walled; stomates few, 4 to 6 at base of capsule, 34-36 (38) µm long; opercula rostrate, 0.5-1.5 mm long; annulus of 1-2 rows of thick-walled, hyaline cells, fragmenting; peristome teeth red, vertically striate, ±0.5 mm long, 40-50 (60) µm wide at base, divided 1/2 way down into 2 segments;

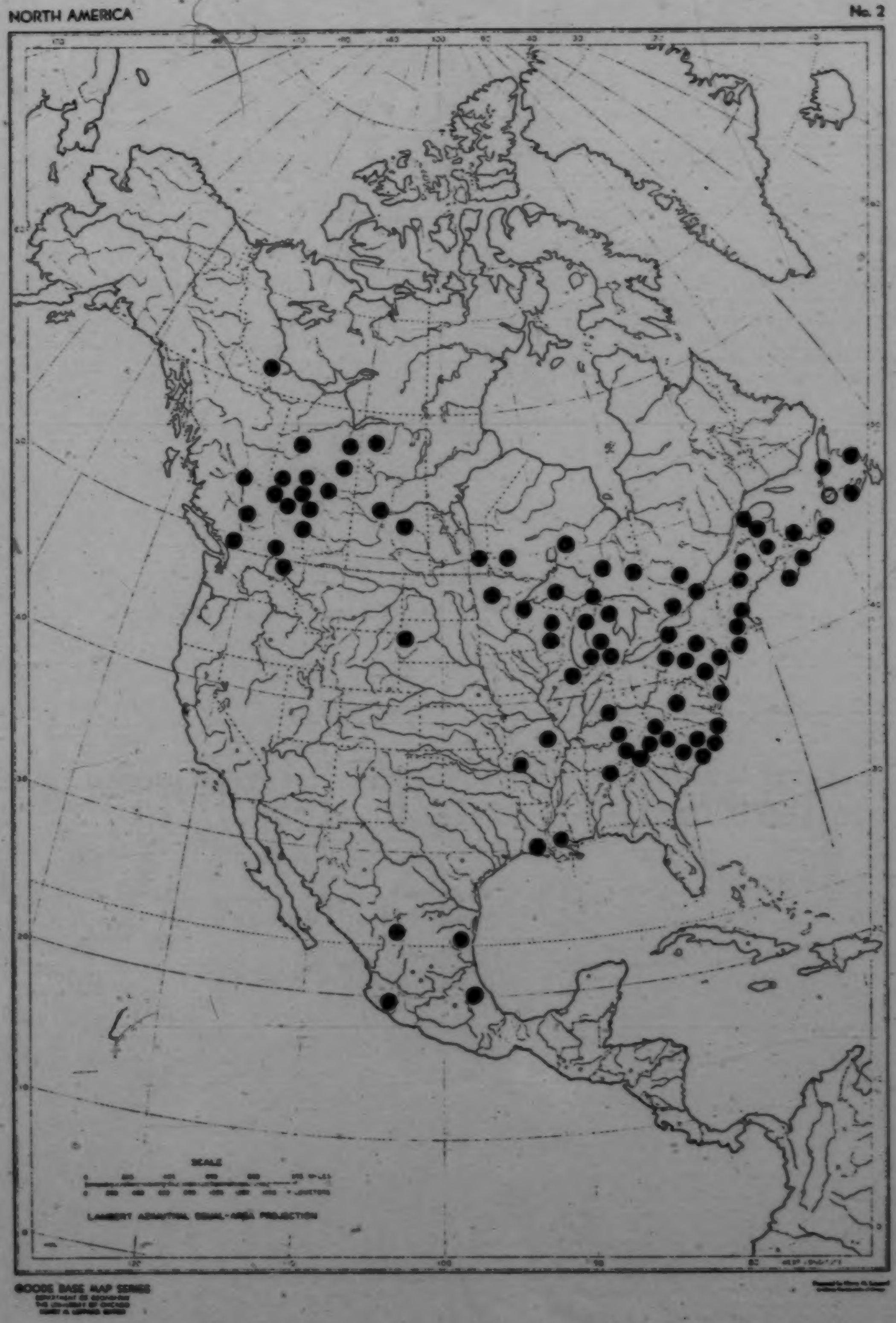
spores green to brown, lightly papillose, 10-13 (15) µm. Chromosome number, n=12, 23.

Habitat and Distribution (Fig. 13): This species is found growing on logs and stumps in moist, shaded deciduous forests. In Alberta it commonly occurs on logs of *Populus tremuloides* Michx. and *Populus balsamifera* L. and rarely grows on logs of such coniferous species as *Picea glauca* or *Pinus banksiana* which are often found in the same area. Occasionally sizeable colonies of *O. flagellare* will be found growing on moist humus around trees or logs.

Orthodicranum flagellare is found throughout the boreal forest wherever angiospermous logs are found. It is common from Newfoundland westward to the mountains of Alberta, British Columbia and the Northwest Territories. In the west it extends southward into Montana and South Dakota while in eastern North America it extends southward through North Carolina and Louisiana into Mexico and the Dominican Republic of the West Indies. It is also reported from Europe, eastern Asia, Siberia, Manchuria, Japan, Korea, and the Canary Islands.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal., 82 (DUKE, NY, FH, CANM). Drummond, Musci Amer. (Rocky Mtns.) 81 as *D. strictum* (NY, FH, CANM). Gray and Sull., Musci Alleg., 162 (NY, FH). Grout, North American Musci Perf., 141 (DUKE, FH, MICH, CANM). Holzinger, Musci Acroc. Bor. Amer., 103 (DUKE, CANM, MICH), 103b

FIGURE 14. The North American distribution of *Orthodicranum flagellare* (Hedw.) Loeske.


NORTH AMERICA
No. 2
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO

(CANM). Macoun, Can. Musci, 34(NY), 36(NY, CANM, MICH), 52(MICH). Renauld and Cardot, Musci Amer. Sept., 5(FH, CANM), 7(NY). Sull. and Lesq., Musci Bor. Amer. (ed. I) 56(DUKE, NY, FH, MICH), (ed. II) 72(FH).

CANADA. Alberta: 9.7 km N of Fort Saskatchewan, Turner 10008 (ALTA). Ft. McMurray, about 42 km N of town, near Syncrude camp, Peterson and Douglas 4462 (ALTA). Touchwood Lake area, 111°26'W, 54°51'N, Vitt 17372 (ALTA). Rocky Mtn. House area, 14.3 km S of Saskatchewan River on Hw. 11, Horton 6821 (ALTA). Two Lakes Region, 27.2 km N of Two Lakes, Peterson 1265 (ALTA). British Columbia: Edgewood, MacFadden 2024 (F). Prince George, Frye 3179 (COLO). Manitoba: Near Ontario border, Hw. 1, Hand 1069 (MICH). New Brunswick: Westmorland Co. 6.5 km NW of Sailsbury, Ireland 13487 (ALTA). Restigouche Co., 47°46'N, 67°13'W, Ireland 14453 (ALTA). Newfoundland: Grand Falls, Habeeb 897 (MICH). Nova Scotia: Cape Breton Island, Macoun, July 14, 1898 (NY). Shelburne Co., 43°59'N, 65°26'W, Ireland 12232 (ALTA). Ontario: Blue Lake Prov. Park, 8.9 km N of Vermilion Bay, Vitt 4488 (ALTA). Lake Timagami, Taylor 3272 (MICH). Pine Hill, Rockcliffe Park, Ottawa, Macoun 90 (DUKE). Prince Edward Island: Queens Co., Strathgarthna Park, 46°12'N, 63°21'W, Ireland 13719 (ALTA). Quebec: Kamourasha Co., Ste. Anne, LePage 230 (DUKE). Gatineau Park, Luskville Falls, 45°32'N, 76°00'W, Peterson 2398 (ALTA). Pontiac Co., 45°48'N, 76°15'W, Ireland 16016 (ALTA). Saskatchewan: Prince Albert Nat. Park, Waskesi Lake, Koponen 25110 (ALTA). Melfort Dist. Candle Lake, Mosquin 1 (ALTA).

U.S.A. Alabama. Marion Co., Hackleburg, Anderson 20195 (MICH). DeKalb Co., Little River Canyon, Sharp and Anderson 582 (CANM). Iowa: Allamakee Co., Old Stone House, Conrad 10 (MICH). Illinois: Berwyn, Calkins 5819a (MICH). Kentucky: Oldham Co., near Lake Louisville, Crum 2596 (CANM). McCreary Co., Cumberland Falls State Park, Norris 63-164a (TENN). Louisiana: Livingston Co., 4.9 km ENE of Port Vincent, Reese 10544 (DUKE). Lafayette Co., 16 km N of Bastrop, Reese 2007 (CANM). Maine: Piscataquois Co., Baxter Peak cutoff, Hermann 19544 (DUKE). Maryland: Worcester Co., 14.6 km NW of Snow Hill, Reese 7398 (CANM). Michigan: Emmet Co., 5 Mile Creek, Snider 871 (DUKE). Mackinac Co., Boris Blanc Isle, Steere, July 8, 1942 (MICH). Van Buren Co., South Haven, Schnoeberger 73 (MICH). Minnesota: Clearwater Co., Itasca State Park, Olson 538 (ALTA). Mississippi: Talahachi Co., 9.7 km N of Charleston, Anderson 4438 (DUKE). Missouri: Warren Co., Just E of Hopewell, Redfearn and Redfearn 28412 (ALTA). Montana: Columbia Falls, Williams 35 (F). New Hampshire: Plymouth, Langdon 19 (MICH). New Jersey: Flatbrook, Bartram *et al.*, 6569 (COLO). New York: Long Island, Cold Springs Harbour, Cain, Aug. 17, 1936 (MICH). Buffalo, Clinton s.n. (MICH). North Carolina: Granville Co., 0.4 km E of Goshen, Baston 515 (DUKE). Hartford Co., 6.5 km E of Murphiesboro, Anderson 5719 (DUKE). Yancz Co., Ramseytown, Anderson 15193 (DUKE). Pennsylvania: Pike Co., Eich's Pond, Lewis 3332 (MICH). Warren Co., Sheffield, Morris and Berd 17271 (MICH). Tennessee: Blount Co., Cade's Cove, Sharp 34758 (CANM). Virgina: Blacksburg, Cottam 4534 (COLO). Wisconsin: Portage

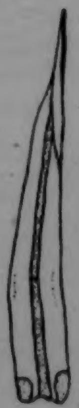
Co., New Hope, Becker 742 (MICH). Douglas Co., Koch 5824 (MICH). Lincoln Co., Freckman 433 (MICH).

Orthodicranum flagellare is the most widespread member of the genus in North America. It grows on logs and stumps and occassionally on humus at the base of trees, often in mats several feet in diameter. When the stiff flagellated branches are present, it should not be confused with any other species, since these structures are usually very noticeable and diagnostic. When these branches are missing, the species might be confused with *O. montanum* or sterile *Dicranum fuscescens*. *Orthodicranum flagellare* differs from *O. montanum* by larger size (*O. montanum* is usually <1.5 cm tall while *O. flagellare* is >2.0 cm tall) and leaves that are never strongly crisped. Microscopically it lacks papillae on the abaxial surface of the upper lamina. *Orthodicranum flagellare* has tubulose leaves (Fig. 15-14) and should be easily separated from *Dicranum fuscescens* which has the costa producing a keel on the abaxial surface of the leaf (Fig. 27-13).

Two synonyms of *O. flagellare* were described from specimens collected in eastern North America, the type of *Dicranum miquelonese* is from Miquelon Island and is a sterile specimen without any flagellated branches. Renauld and Cardot (1889) suggested that it was related to *D. elongatum* due to growth habit and described it as new because it differed from *D. elongatum* by its areolation. They did mention that it was probably also related to *D. flagellare*. After

FIGURE 15. *Orthodicranum flagellare* (Hedw.) Loeske

1-4	Stem leaves (14x)
5, 6	Flagelliform branch leaves (14x)
7	Perichaetial leaf (14x)
8	Upper laminal cells (280x)
9	Median laminal cells (280x)
10	Basal laminal cells (280x)
11, 12	Capsules (10x)
13	Peristome tooth (180x)
14	Median transverse-section (280x)



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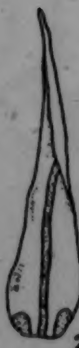

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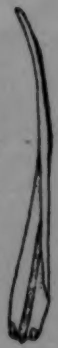

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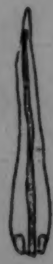

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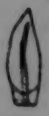

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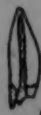

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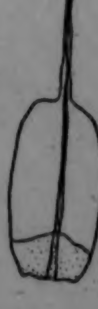

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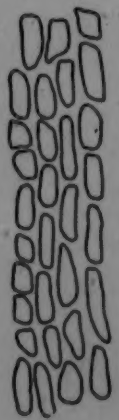

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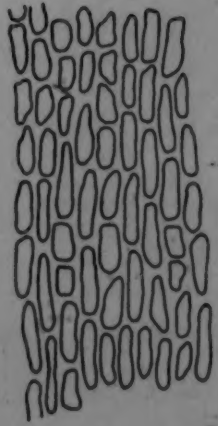

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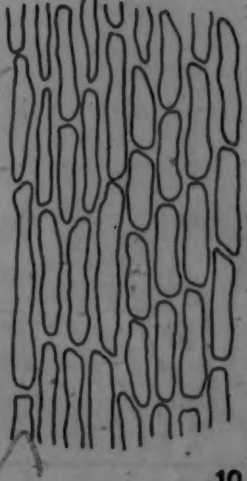

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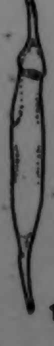

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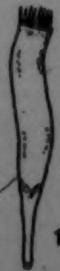

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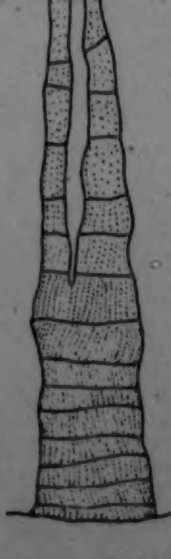

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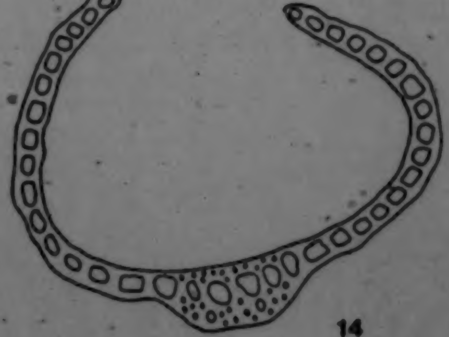


14

examining the specimen, I consider it to be within the limits of the concept of *Orthodicranum flagellare*, although the leaves are more falcate-secund than normally seen and the growth habit is somewhat more compact than normal. *Dicranum crispatulum* (Röll) Kindb. originally described as *D. miquelonense* var. *crispatulum* Röll from a New Jersey specimen, is little different from the Miquelon Island specimen except for slightly crisped leaves (a character state common in *O. flagellare*) and, in my opinion, differs even less from normal forms of *Orthodicranum flagellare*.

2. *Orthodicranum montanum* (Hedw.) Loeske, Stud. Morph. Syst. Laubm. 85. 1910.

Dicranum montanum Hedw., Sp. Musc. 143. 1801.

Type: *"In montium ed. torum truncis putridis legit Ludwig, in Silesiae monte Tafelfichte."* (Lectotype-G!)

Scytalina montanum (Hedw.) Hagen, K. Norsk. Vid. Selsk. Skrift. 1914 (1) 132. 1915.

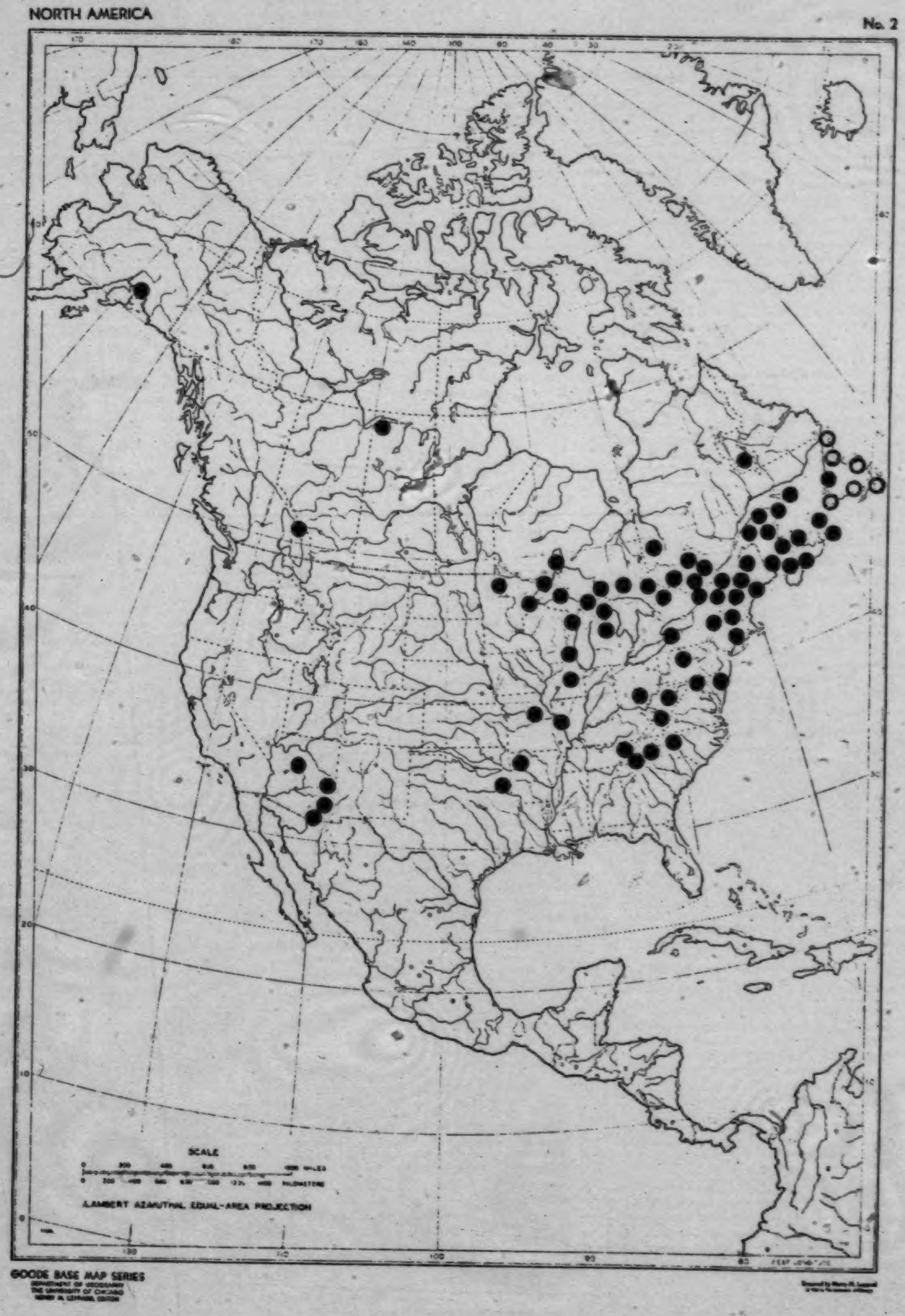
Plants small to minute, up to 3.5 cm tall, in loose to dense mats, light-green, growing on logs or living trees. Stems lightly tomentose, tomentum white to brown. Leaves when dry strongly crisped, when moist contorted or falcate-secund, not undulate, (1.0) 1.5-3.5 mm long, narrowly lanceolate, tapering to a sharply acute tip, tubulose or slightly keeled in upper 1/3, papillose on upper 1/2 of abaxial surface; margins serrate to entire, unistratose; costa narrow,

(18) 25-30 (40) µm wide just above alar region, percurrent or slightly excurrent, slightly toothed or papillose on abaxial surface, costa in median transverse-section showing 3 to 5 guide cells and 2 weak stereid bands, both bands extending into upper 1/3 of leaf, each band composed of one or two cell layers, neither abaxial or adaxial layer of external cells differentiated from stereid cells; alar cells brown, unistratose, often reaching costa; basal cells just above alar region, rectangular, thin-walled, smooth, not pitted, cell ends rounded or square, (16) 25-40 (50) µm long, median cells quadrate to short-rectangular, (6.0) 8.0-14 µm long, thin-walled, smooth, not pitted, in rather uniform rows, upper cells similar to median. Perichaetial leaves as long as vegetative leaves and abruptly acuminate into a subulate tip.

Dioicous, male plants similar to the female ones. Monosetous, setae yellow to brown, 0.4-1.5 (1.8) cm long. Capsules yellow to dark-brown, erect, short-cylindric, 1-2 mm long, lightly wrinkled, constricted below the mouth, neck short; exothecial cells rectangular, thin-to thick-walled, angled; stomates few, in single row at base of capsule, 24-30 µm long; opercula rostrate, 0.5- 1.0 mm long; annulus of 1 to 3 rows large, hyaline, thick-walled cells, fragmenting; peristome teeth orange to red, vertically striate, ±0.5 mm long, 30-45 µm wide at base, divided 1/2 to 2/3 down into 2 segments; spores green, papillose, thick-walled, 10-14 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 16): Specimens of *Orthodicranum montanum* are usually found growing as dense woolly mats on logs,

FIGURE 16. The North American distribution of *Orthodicranum montanum* (Hedw.) Loeske


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
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stumps, and tree bases in shaded forests. It occurs from Newfoundland and Nova Scotia in eastern Canada inland as far as northern Minnesota and southward through North Carolina, Missouri, and Arkansas into Mexico. From Mexico it extends upward into the mountains of Arizona and New Mexico. Disjunct collections have been made in the Rocky Mountains of British Columbia, in southern Alaska, and just south of Lake Athabasca in Saskatchewan. It is also reported from Europe and eastern Asia as well as Japan. Takaki (1964) said that these reports from Japan were erroneous, being based on *O. flagellare* specimens; however, in 1972 (Takaki, 1972) he reported finding true *O. montanum* in northern Japan.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appl. 81(DUKE, FH, CANM, NY). Bartram, Mosses Southern Ariz. (FH, CANM). Drummond, Musci Amer. (Rocky Mtns.) 102(NY, FH, CANM). Grout, N.Amer. Musci Perf. 115(DUKE, FH, NY, COLO, MICH, CANM). Holzinger, Musci Acroc. Bor. Amer. 389(DUKE, CANM, MICH), 506 (DUKE, NY, CANM, MICH). Macoun Canadian Musci 34(US, CANM, NY), 51(MICH). Renauld and Cardot, Musci Amer. Sept. 357(FH, MICH, CANM). Sull. and Lesq., Musci Bor. Amer. 55 (DUKE, FH, NY, MICH). Sull. and Lesq. Musci Bor. Amer. Ed. II 71(FH, MICH).

CANADA. British Columbia: Rogers Pass, on rocks, Brinkman, July 5, 1908 (CANM). New Brunswick: Kent Co., 4.9 km W of Rexton, Ireland 14151 (ALTA). Restigouche Co., 0.8 km N of Lorne, Ireland 14388 (ALTA). Charlotte Co., 13 km W of St. Andrews, Ireland 13308 (ALTA).

Newfoundland: Bay of Islands, Aspex Beach, Waghorne, May 27, 1896 (MIN). Anapolis Co., Kejimkujik Nat. Park, Ireland 12602 (ALTA). Labrador, Sable Point, Waghorne, Sept. 15, 1894 (MIN). Nova Scotia: Luneburg Co., 3.2 km No of Aldersville, Ireland 17549 (ALTA). Colchester Co., Upper Brookside, Smith, July 2, 1931 (MICH). Cape Breton Island, Louisberg, Macoun 536 (DUKE). Ontario: Ottawa, Victoria Park, Macoun, Oct. 5, 1907 (DUKE). Thunder Bay Dist., Sibley Peninsula, Garton 2901 (MIN). Algonquin Park, Macoun, June, 1906 (DUKE). Prince Edward Island: Queens Co., Strathgartney Park. Ireland 13723 (ALTA). Quebec: Mt. Shefford, Fabius 2244 (DUKE). Gatineau Park, Luskville Falls area, Peterson 2381 (ALTA). Terrebonne Co., Mt. Tremblant Park, Flowers 5863 (COLO). Anticosti, Victorin and Germain 49611 (MICH). Saskatchewan: Lake Athabasca, south shore, E of William River, Argus 370-72 (CANM).

U.S.A. Alaska: Valdez, Valdez Quadrangle, Hermann 21702 (US). Arizona: Bonita Creek, Goodding 1223 (ARIZ). Appache Co., Phelps Botanical Area, Phillips 3055 (ARIZ). Pima Co., Santa Catalina Mtns. Goodding 10928 (ARIZ). Oak Creek Canyon, Johnsen 773 (MNA), Arkansas: Newton Co., 6.5 km WNW of Jasper, Redfearn 11861 (TENN). Connecticut: New London Co., Vicinity of Norwich, Holdridge, 1946 (MIN). Iowa: Allamakee Co., Abies hillside, Conard, June 27, 1936 (COLO). Illinois: Randolph Co., Vicinity of Piny Creek, Redfearn 23013 (MICH). Maine: Oxford Co., Hartford, Parlin 9515 (DUKE). Norway, Pikers Hill, Bacon 584 (COLO). Kennekec Co., Pittston, Parlin 8415 (DUKE). Maryland: Patuxent Research Refuge, Leonard 20313 (MICH). Michigan: Emmet Co., Nichols 13 (MICH). Sugar Island, Steere 3404 (COLO). Gratiot Co., Schoeberger 400 (MICH). Luce Co., Upper Tahquemenon Falls, Anderson 20046 (DUKE). Missouri: Warren Co., 2.4 km E of Case, Redfearn 28370 (TENN). New Mexico: Cowles, Holy Ghost Canyon, Flowers 725 (COLO). New York: St. Lawrence Co., Cranberry Lake, Catharine Is., Ketchledge 130 (ALTA). Saratoga Co., 49°59'N, 75°03'W, Vitt 5269 (ALTA). North Carolina: Transylvania Co., Lake Foxaway, Culberson 5755 (DUKE). Cherokee Co., Murphy, Anderson 8080 (DUKE). Macon Co., Anderson 8322 (DUKE). Swain Co., Andrew's Bald, Anderson 3286 (DUKE). Avery Co., Grandfather Mtn., Anderson 12719 (DUKE). Ohio: Jackson Co., Bartley and Pontuis, 1937 (MICH). Oklahoma: Leflore Co., Winding Stair Mtn., Redfearn 19688 (SMS). Pennsylvania: Clearfield Co., Clearfield Creek at Dimeling, Pursell 10084 (ALTA). Tennessee: Sevier Co., Mt. LeConte, Sharp 36187 (COLO). Blount Co., Cades Cove, Sharp 34409 (MICH). Vermont: Newfane, Flowers, July 1934 (COLO). Glebe Mtn., Grout, July 28, 1900 (COLO). Across from Colebrook, N.H., Crum and Anderson 7882 (MICH). West Virginia: Marion Co., Fairmont, Lunk, July 6, 1946 (MICH). Pocahontas Co., Gaudineer Knob, Burtt, June 17, 1968 (MICH). Wisconsin: Bayfield Co., Squaw Point, Lake Superior, Flowers 9889 (COLO). Douglas Co., Koch 7485 (MICH). Door Co., Freckman 347 (MICH). District of Columbia: Rock Creek Park, Hermann 14126 (DUKE).

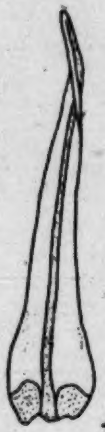
Orthodicranum montanum is, morphologically, the smallest member of the genus, sometimes being no more than 0.2 cm in height. Even when the plants are this small they are quite distinct since they have very crisped leaves (when dry) and prominent papillae on the abaxial surface of the upper lamina and costa. It may occasionally be mistaken for a specimen of *O. flagellare* without the characteristic flagellated branches; however, the leaf papillae and the crisped leaves should separate it. It is closely related to *O. flagellare*, much more so than to any other species. Affinities within *Orthodicranum* are easily seen in costal differentiation (as viewed in transverse-section), with *O. montanum* and *O. flagellare* showing a narrow costa with stereid bands (Figs. 15-14, 17-13) while *O. fulvum* and *O. viride* have a very wide costa with stereid bands (Figs. 19-13, 21-13). In contrast, *O. strictum* lacks stereid bands and is not extremely close in relationship to the other four species.

Takaki (1964) summarized the characters used to separate *O. montanum* and *O. flagellare* stating that the latter has secund or crispate leaves, smooth upper cells that are irregularly areolated and smooth or slightly rough, and very short and quadrate lower cells. In contrast, *O. montanum* has crispate or woolly leaves, regularly quadrate or short-rectangular cells that are mamillose and lower cells that are rounded and elongate-rectangular. He also stressed the flagellated branches found in *O. flagellare*.

I believe the flagellated branches, crispate leaves, and papillae to be the most significant characters in separating *O. montanum* from

FIGURE 17. *Orthodicranum montanum* (Hedw.) Loeske.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9,10	Capsules (10x)
11	Peristome tooth (180x)
12	Transverse-section thru alar region (280x)
13	Median transverse-section (280x)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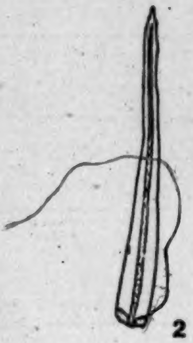
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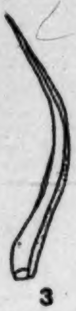
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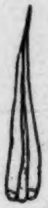
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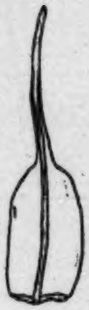
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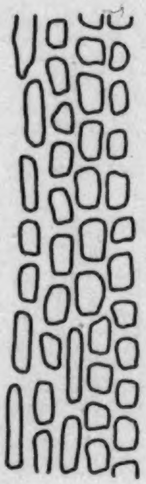
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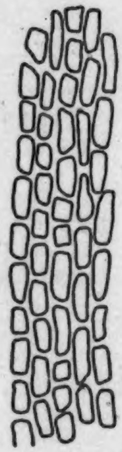
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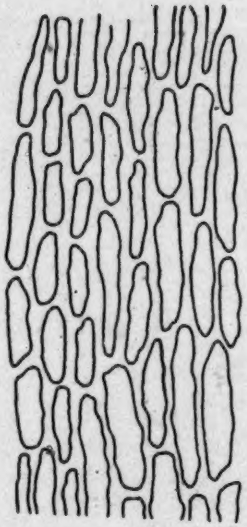
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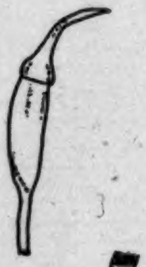
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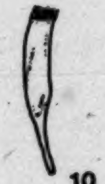
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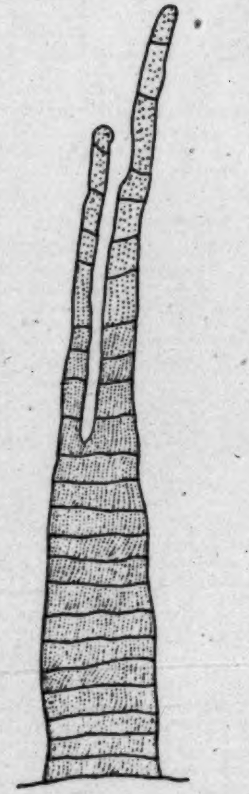
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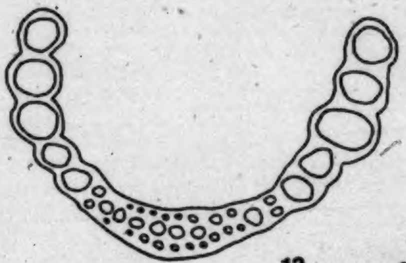
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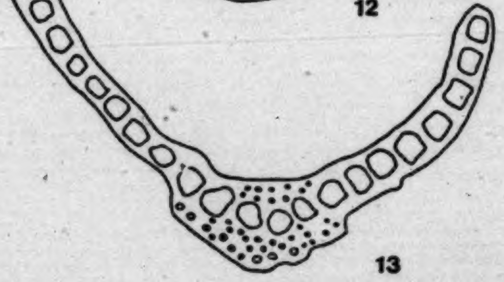
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O. flagellare. The upper cells of *O. montanum* may occasionally be slightly mamillose but this is not always true. Also, there is intergradation between cell shapes and sizes in the two species and I would put little weight on these points. Although there seems to be only a few characters separating these two species, they are quite distinct and should seldom be confused.

3. *Orthodicranum fulvum* (Hook.) Roth. *ex* Cas. Gil., Fl. Iber. Musg. 176. 1932.

Dicranum fulvum Hook., Musci Exot. 2. 149. 1819.

Type: "Nova Scotia. D. Menzies, 1785." (Holotype-BM!)

Paraleucobryum fulvum (Hook.) Loeske, Hedwigia 49: 23. 1910.

Dicranum interruptum Brid., Spec. Musc. 1: 179. 1806. *Hom. illeg., non Dicranum interuptum* Hedw., Spec., Musc. 129. 1801.

Plants small, up to 4.0 cm tall, in loose mats, dark-green, dull, growing on rock or occassionally on soil. Stems lightly tomentose, tomentum light-to dark-brown. Leaves when dry, slightly twisted or sometimes falcate-secund, when moist, usually erect and slightly imbricate, not undulate, 2.5-5.0 mm long, narrowly lanceolate, tapering to a sharply acute tip, tip sometimes broken, tubulose or slightly keeled, adaxial and abaxial laminal surfaces smooth, margins unistratose; costa wide, 90-120 µm (1/4 to 1/3 width of leaf base) wide, excurrent, sometimes filling the upper 1/3 of leaf tip, smooth or slightlypapillose on upper abaxial surface, costa in median transverse-section showing 10 to 14 guide cells with 2 well developed stereid bands, both extending well into the leaf apex, each band composed of 2 to 3 rows of strongly thickened cells, both adaxial and abaxial layer of external cells differentiated from stereids by large lumens. Alar cells brown to red-brown, unistratose, often reaching costa; basal cells just above alar region rectangular, 15-30 μm long, quickly changing to quadrate or short-rectangular median cells, median cells in rather uniform rows, 5.0-16 μm long, not pitted, upper cells similar to median. Perichactial leaves much larger than vegetative leaves, abruptly acuminate to a long subulate tip.

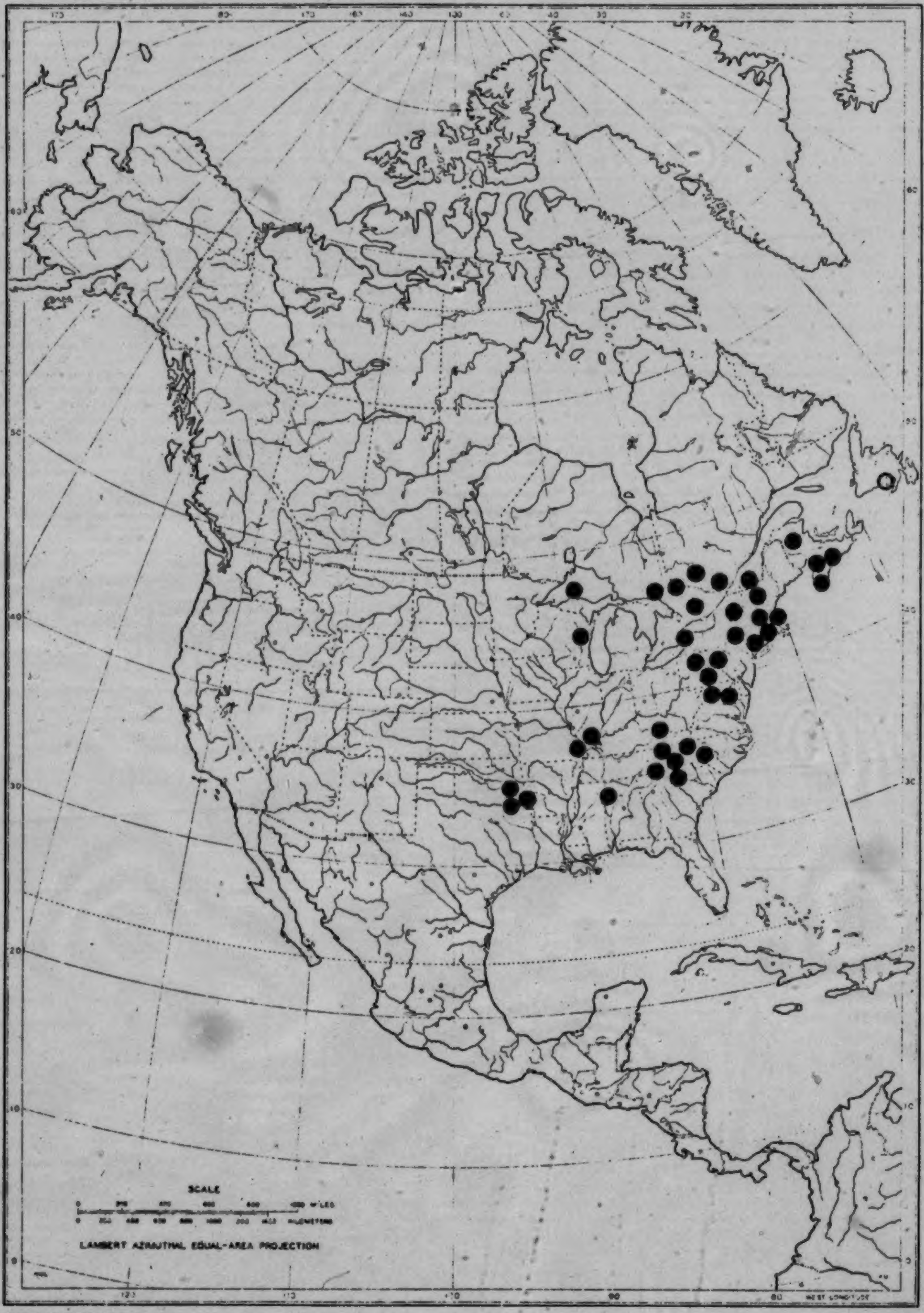
Dioicous, male plants as large as or slightly smaller than female ones. Monosetous, setae yellow to brown, (0.6) 1.0-2.5 cm long. Capsules light-brown, erect, short-cylindric, 1.0 - 2.5 mm long, smooth or slightly wrinkled, somewhat constricted below the mouth, neck short; exothecial cells triangular to rectangular, thick-walled; stomates few, in one row at base of capsule, 30-35 μm long; opercula rostrate, 1.5 — 2.5 mm long; annulus of 1 to 2 rows of large, hyaline, thick-walled cells, fragmenting; peristome teeth orange to red, vertically striate, about 0.3 mm long, 40-50 μm wide at base, divided 1/2 to 2/3 down into 2 segments; spores green to light brown, lightly papillose, thin walled, 16-25 μm. Chromosome number unknown.

Habitat and Distribution (Fig. 18): *Orthodicranum fulvum* typically grows on siliceous rocks in eastern North America. It usually does

FIGURE 18. The North American distribution of *Orthodicranum fulvum* (Hook.) Roth.

NORTH AMERICA

No. 2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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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best in areas with a moderate light intensity and a moderate substrate slope (Seltzer and Wistendahl, 1971) such as that usually found on rocks in ravines or along streams in deciduous forests. The species occurs from Nova Scotia westward into Ontario and Wisconsin, and southward into South Carolina, Alabama, and Oklahoma. In addition, it has been reported from Europe, Japan, and Korea.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 83 (DUKE, NY, FH, MICH, CANM). Drummond, Musci Amer. (Rocky Mtns) 49 (DUKE, FH), 93 (MICH, CANM). Gray and Sull. Musci Allegh. 159 (DUKE, FH). Grout, N. Amer. Musci Perf. 21 (MICH, CANM). Holzinger, Musci Acroc. Bor. Amer. 104 (DUKE, NY, MICH, CANM). Macoun, Can. Musci 37 (MICH, CANM). Small, Mosses of So. U.S. 68 (DUKE). Sull. and Lesq., Musci Bor. Amer. 57 as *D. interuptum* (DUKE, FH). Sull. and Lesq. Musci Bor. Amer. Ed. II. 73 as *D. interuptum* (FH).

CANADA. New Brunswick: York Co., 3.2 km N of Tweedside, Ireland 13064 (ALTA). Nova Scotia: Halifax Co., Porters Lake, Ireland 12108 (ALTA). Annapolis Co., 4.9 km S of Bridgetown, Ireland 17755 (ALTA). Ontario: Hastings Co., 9.7 km N of Gunter, Ireland 16279 (ALTA). Jordon, Crum 133 (MICH). Sudbury, Cain 3346 (MICH). Algonquin Prov. Park, 45°35'N, 78°29'W, Ireland 15745 (ALTA). Quebec: Gatineau Park, Luskville Falls, Peterson 2387 (ALTA). Pontiac Co., 46°48'N, 76°15'W, Ireland 15996 (ALTA).

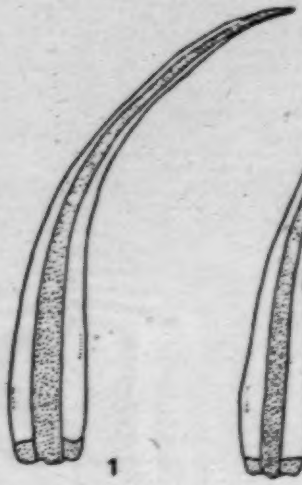
U.S.A. Arkansas: Polk Co., Ouachita Mtns., N of Athens, Anderson 11468 (DUKE). Connecticut: Weston, Valley Forge, Allen and Stair 73 (MICH). Georgia: Marion Co., 11.3 km E of Hamilton, Anderson 15346 (DUKE). Macon Co., Steere 10138 (MICH). Illinois: Gallatin Co., Pounds Hallow, Sadler 16 (ALTA). Kentucky: Wolfe Co., Sky Bridge, Vitt 5006 (ALTA). Massachusetts: Worcester, Greenwood 10 (DUKE). Norton, Rice, April 7, 1942 (DUKE). Amesbury, Huntington, May 2, 1899 (DUKE). Michigan: Keweenaw Co., Keweenaw Point, Richards 97 (MICH). Missouri: Perry Co., Perryville, Demetrio 1894 (MIN). New Hampshire: Marlow, Allen and Stair 73 (MICH). New York: Essex Co., Adirondack, Redfearn 13499 (MICH). St. Lawrence Co., Barber Point, Breisch 16 (ALTA). North Carolina: Jackson Co., Wolf Creek, Anderson 10183 (DUKE). Macoun Co., Highlands, Sharp 34664 (DUKE). Orange Co., Duke Forest, Anderson and Powell 12667 (DUKE). Alexander Co., Hiddenite, Anderson 7590 (DUKE). Oklahoma: McCurtain Co., Redfearn 19848 (SMS). Leflore Co., Cedar Creek Lake, Redfearn 24737 (SMS). South Carolina: Pickens Co., Pinnacle Mtn., Duncan 13935 (DUKE). Tennessee: Sevier Co., Mt. LeConte, Sharp 341039 (MICH). Vermont: across from Colebrook, N.H., Crum and Anderson 7912 (MICH). Virginia: Page Co., Blue Ridge Mtns., Shanandoah Nat. Park, Flowers 4646 (COLO). Prince William Co., Prince William State Forest, Ireland 2069 (CANM). Wisconsin: Sauk Co., Hawksnest, Boulder Field, Armstrong 49 (MICH). District of Columbia: Rock Creek, Holzinger, May 8, 1892 (UC).

At times, *Orthodicranum fulvum* may be confused with either *O. viride* or *Dicranum fuscescens*. The significant differences (Table 5) between these three are considerable and reasonable care should prevent problems. The erect capsules easily distinguishes both *O. fulvum* and *O. viride* from *D. fuscescens*; however, sterile material is very common and gametophytic criteria must be used to separate them in such cases. The narrow costa (Fig. 27-13) and long-rectangular basal cells (Fig. 27-8) of *D. fuscescens* are quite different from the broad costa (Figs. 19-13, 21-13) and quadrate to short-rectangular basal cells (Figs. 19-9, 21-8) of the two *Orthodicranum* species. *Dicranum fuscescens* also has bistratose alar regions while all members of *Orthodicranum* have unistratose alar regions.

Orthodicranum fulvum traditionally differs from *O. viride* by having intact leaf tips while the latter has broken tips that serve as vegetative reproduction structures. This can rarely lead to misidentification since *O. fulvum* occasionally has broken leaf tips (Fig. 19-5), but they are not broken to the extent of those in *O. viride* (Fig. 21-3). Also, the basal cells of *O. fulvum* (Fig. 19-9) are considerably shorter than those of *O. viride* (Fig. 21-8) and most importantly, the habitats are extremely different. *Orthodicranum fulvum* is the only species in the genus to be found primarily on rocks and *O. viride* is the only species to occur primarily on living angiosperm trees.

FIGURE 19. *Orthodicranum fulvum* (Hook.) Roth.

1-5	Stem leaves (14x)
6	Perichaetial leaf (14x)
7	Upper laminal cells (280x)
8	Median laminal cells (280x)
9	Basal laminal cells (280x)
10, 11	Capsules (10x)
12	Peristome tooth (180x)
13	Median transverse-section (280x)



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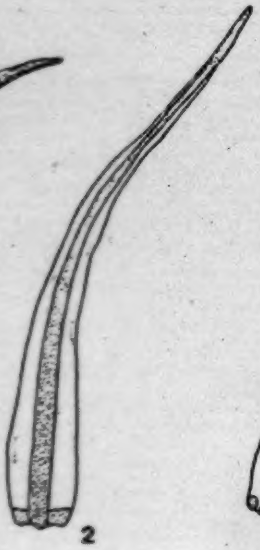

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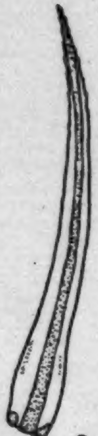

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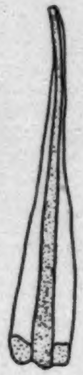

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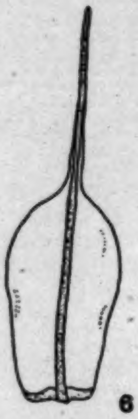

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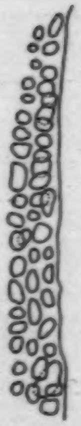

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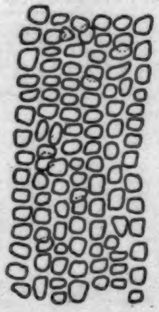

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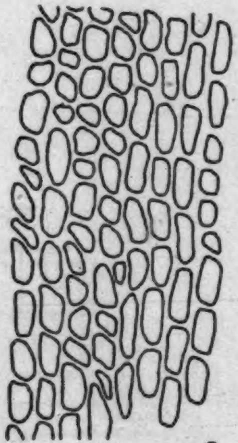

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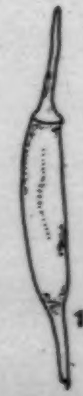

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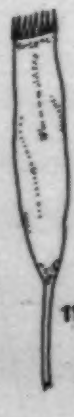

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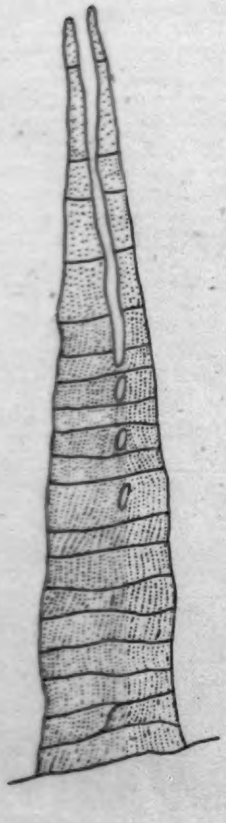

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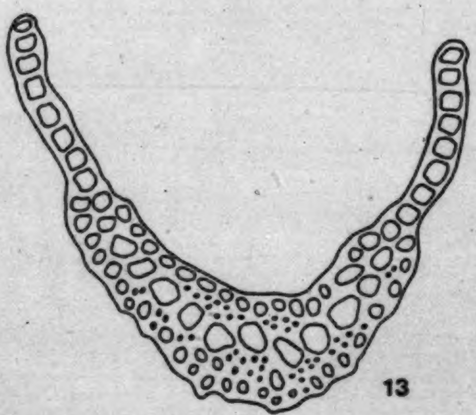

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TABLE 5. Distinguishing character states of *Orthodicranum fulvum* (Hook.) Roth , *O. viride* (Sull.) Roth and *Dicranum fuscescens* Turn.

	O. fulvum	*O. viride*	*D. fuscescens*
1. Costa width (% of leaf base)	35-50%	20-30%	<20%
2. Common habitat	rock	living trees	logs
3. Colour	dark-green to brown	light-green	dark-green to brown
4. Basal cell shape	± quadrate	rectangular	long-rectangular
5. Margins	serrate	± entire	strongly serrate
6. Leaf tips	± intact	broken	intact
7. Leaf arrangement	falcate-secund	± straight	falcate-secund
8. Capsule orientation	erect	erect	curved
9. Alar cells	unistratose	unistratose	bistratose
10. Papillae	present	seldom present	usually present

4. *Orthodicranum viride* (Sull. et Lesq.) Roth *in* Cas. Gil, Fl. Iber. Musg. 176: 64 c-e 1932.

Campylopus viridis Sull. et Lesq., Musci Boreli-Americani No. 72. 1856.

Type: *"In sylvis ad truncos putridos, a Nova Anglis usque ad Ohionen, haud rarum, semper sterile."* (Lectotype-FH-SULL!, Isotypes-FH!, NY!)

Dicranum viride (Sull. et Lesq.) Lindb., Hedwigia 2: 70. 1863.

Dicranum fulvum Hook. ssp. *viride* (Sull. et Lesq.) Lindb., *in* Hartm., Handb. Skand. Fl. ed. 9(2): 68. 1864.

Dicranum fulvum Hook. var. *viride* (Sull. et Lesq.) Frye *in* Grout, Moss Fl. N. Am. 1(2): 80. 1937.

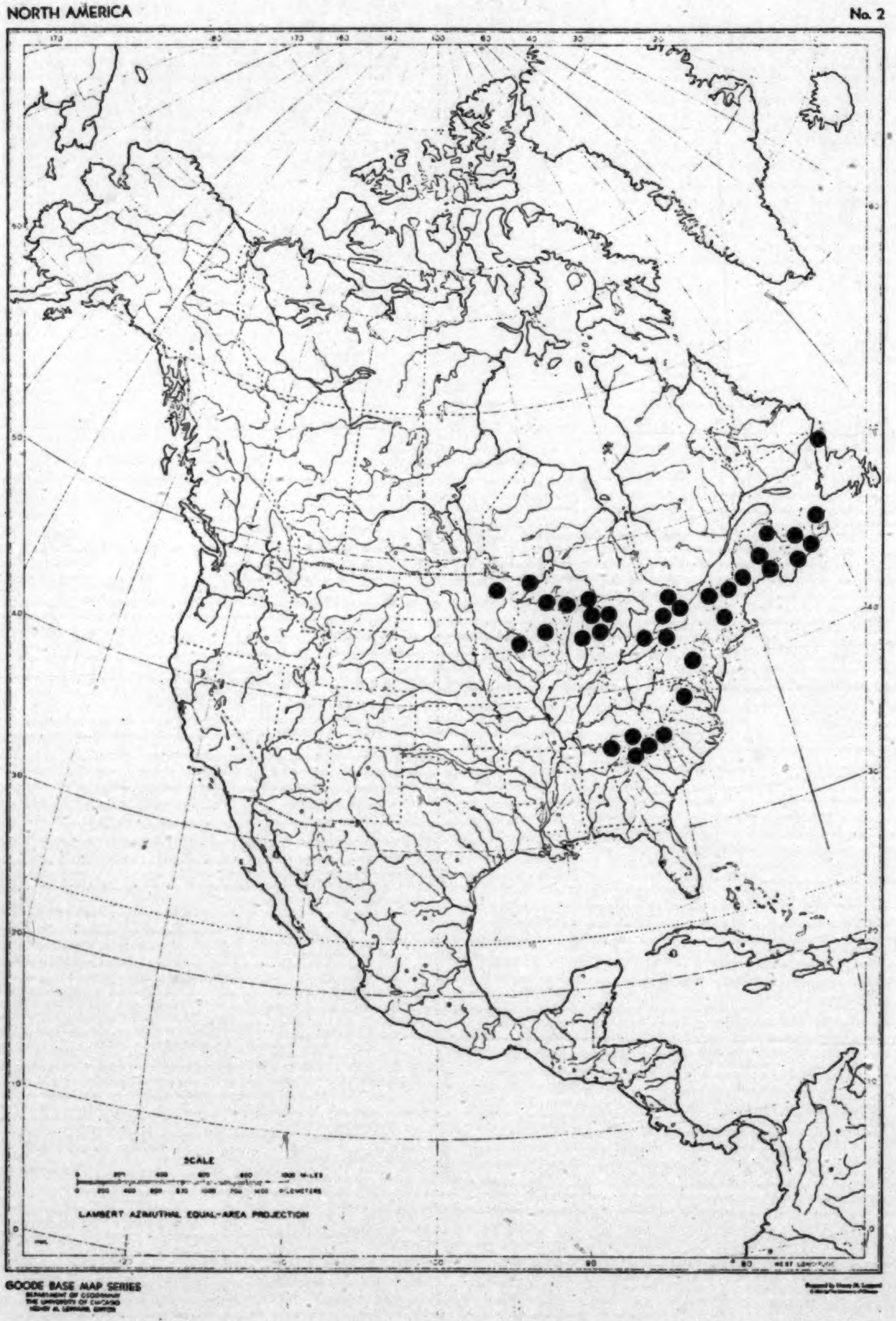
Paraleucobryum viride (Sull. et Lesq.) Podp., Consp. 153: 1954.

Plants small, up to 2.5 cm tall, in small tufts or small patches usually growing on trees, light-green, shiny. Stems lightly tomentose, tomentum light-to dark-brown. Leaves when dry, erect, imbricate, not undulate, similar when moist, 1.5-4.0 (5.0) mm long, narrow-lanceolate, tapering to an acute tip, tip usually broken, tubulose or rounded, rarely slightly keeled, lamina smooth, margins unistratose, sometimes bistratose in upper 1/4, entire; costa wide (100) 110-130 µm just above alar region, excurrent, sometimes filling upper 1/4 of leaf, smooth on both adaxial and abaxial surfaces, costa in median transverse-section showing 10-14 guide cells with 2 well developed stereid bands, both extending well into the leaf apex, both adaxial and abaxial layer of external cells well differentiated from stereids by large lumens. Alar cells red to brown, unistratose, often reaching costa, basal cells above alar region long-rectangular, 25-65 µm long, thin-walled, median cells in rather uniform rows, 10-20 (25) µm long, walls smooth, not pitted, upper cells similar to median. Perichaetial leaves slightly larger than vegetative leaves, abruptly acuminate to a long, subulate tip.

Dioicous, male plants as large as or slightly smaller than female ones. Sporophytes rare. Monosetous, setae yellow to brown. (0.5) 1.0-2.0 cm long. Capsules light-brown, erect, short-cylindric, 1.0 - 2.0 (3.0) mm long, smooth or slightly wrinkled, usually constricted below the mouth, neck short; exothecial cells irregular, angled, thick-walled; stomates in one row at base of capsule, 30-35 µm long; opercula rostrate 1.0-2.5 mm long; annulus of 1 to 2 rows of large hyaline, thick-walled cells; peristome teeth orange to red, vertically striate, about 0.3 mm long, 35-50 µm wide at base, divided half way down into 2 segments; spores green to light-brown, lightly papillose, 16-25 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 20): *Orthodicranum viride* is the only species in the genus that usually grows on living trees and it seems to be collected most commonly from the base (usually within 2 metres of the ground) of angiospermous trees instead of coniferous species. This is different from *O. strictum*, the other species that commonly has broken leaf tips and occurs in western North America, which usually grows on conifers trees or logs. Specimens of *O. viride* are sometimes found on logs, but this is not the primary habitat. The species occurs

FIGURE 20. The North American distribution of *Orthodicranum viride* (Sull.) Roth.


NORTH AMERICA
No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
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in eastern North America from Newfoundland westward into Minnesota, and southward along the Appalachian Mountains into North Carolina and Tennessee. It is also reported from Europe and Japan.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 73 (DUKE, NY, FH, MICH, CANM). Holzinger Musci Acroc. Bor. Amer. 8 (DUKE, CANM), 388 (DUKE, CANM). Macoun, Can. Musci 35 (MICH, CANM). Renauld and Cardot, Musci Amer. Sept. 274 (FH, CANM). Sull. and Lesq., Musci Bor. Amer. (ed. II) 91 as *Campylopus viridis* (FH).

CANADA. New Brunswick: Woodstock, Macoun 93 (US). Kent Co., , 21 km S of Harcourt, Ireland 14248 (ALTA). Charlotte Co., 9.7 km S of Rollingdam, Ireland 17092 (ALTA). Nova Scotia: Inverness Co., Cape Breton Highlands Nat. Park, Ireland 12084 (CANM). Colchester Co., 4.9 km S of Lynn, Ireland 17329 ((ALTA). Ontario: Bellville, Macoun 1870 (MICH). Grimsby, Crum 173 (MICH). London, near Nixon's Pond, Dearness, April, 1889 (CANM). Prince Edward Island: Queens Co., Strathgartney Park, Ireland 13769 (CANM). Quebec: Gaspesian Park, Mt. Albert, Crum and Williams 10675 (MICH).

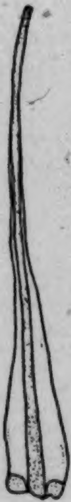
U.S.A. Iowa: Winneshiek Co., Hesper, Conard 7-141 (MICH). Maine: Norway, Bacon, Nov. 13, 1931 (COLO). Michigan: Cheboygone Co., Nichols and Ehlers, June 30, 1920 (MICH). Houghton Co., near Houghton, Richards 25 (MICH). Chippewa Co., Steere 3313 (MICH) Macosta Co., Craton, Schnoeberger 134 (MICH). Minnestoa: Winona, Breton, May, 1894 (DUKE). Basswood Lake, Holzinger, June 12, 1897 (DUKE). Cook Co., Grand Portage Is., Holzinger, Aug. 11, 1902 (MIN). New Hampshire: Jackson, Allen, July 4, 1880 (MICH). New York: Adirondack Mt. Reserve Britton Sept. 13, 1900 (MICH). Buffalo, Clinton s.n. (MICH). North Carolina: Highlands, Anderson 20893 (DUKE). Plaque Trail, Kilmer 8128 (DUKE). Sparta, Anderson 13109 (DUKE). Linville, Schallert M1204 (DUKE). Tennessee: Blount Co., Near Gregory's Bald, Sharp 38130 (FH). Johnson Co., Shady Valley Bog, Sharp 34539 (FH). Vermont: Newfane, Costello 471 (UTC). Wisconsin: Marathon Co., Rib Mtn., near Wausau, Forman E184 (CANM).

Orthodicranum viride is the only species of *Orthodicranum* that has fragile leaf tips, a wide costa that fills about 1/4 to 1/3 of the leaf base, and grows on living trees in eastern North America. It may occasionally be confused with *O. strictum* or *Dicranum fragilifolium*, two other species with fragile leaf tips; however, these species both have a narrow costa that fills about 1/7 to 1/4 of the leaf base. In addition, *D. fragilifolium* has a bistratose alar region and, when fertile, has a curved capsule which distinguishes it from all *Orthodicranum* species. Also, *O. strictum* grows primarily on logs and trunks of trees in western North America; thus, the distribution of these two species does not overlap at any point.

Most taxonomic difficulty involves the close relative, *O. fulvum*. In fact, Williams (1913) considered *O. viride* to be a synonym of his concept of *Dicranum fulvum* (now *O. fulvum*) and Grout (1937) considered

FIGURE 21. *Orthodicranum viride* (Sull. *et* Lesq.) Roth.

1-4	Stem leaves (14x)
5	Perichaetial leaf
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Upper transverse-section (280x)
13.	Median transverse-section (280x)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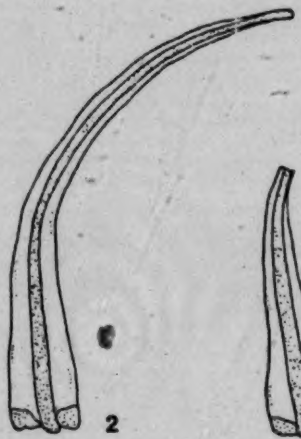
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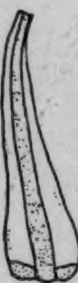
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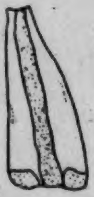
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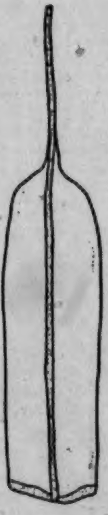
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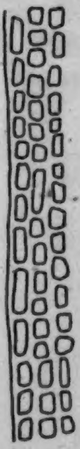
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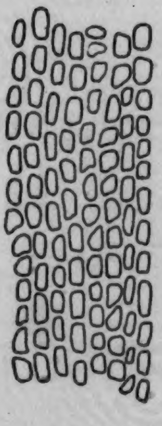
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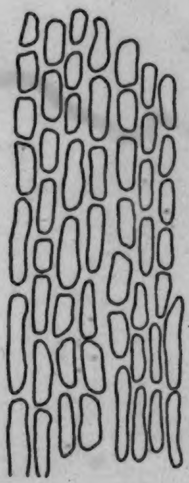
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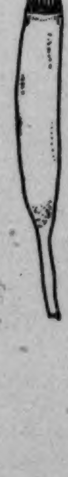
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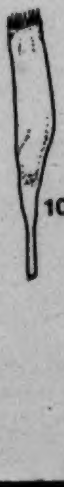
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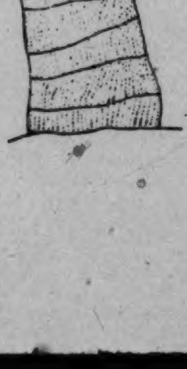
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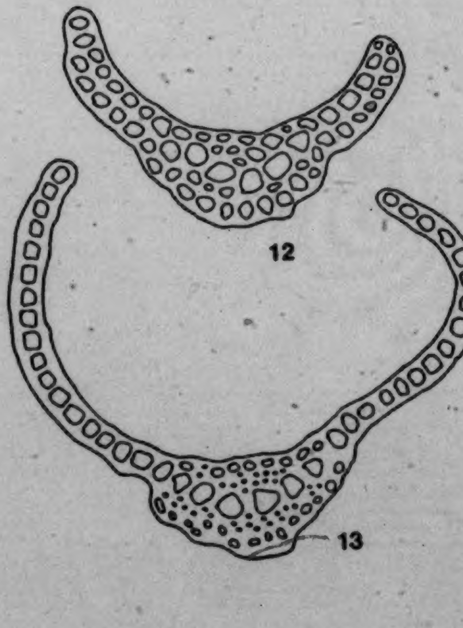
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O. fulvum as a variety. Reimers (1938) dealt with this problem and concluded that both warranted specific status, using size, leaf luster, leaf brittleness, and costa width as the separating criteria. Accordingly, *O. viride* has plants around 2 mm tall or less with leaves that are glossy, straight and have a brittle tip, and its costa is less than 1/3 the leaf base width. *Orthodicranum fulvum* has taller plants (up to 5 cm) with dull, crisped leaves that seldom have broken tips and the costa is more than 1/3 the width of the leaf base. I agree with these differences except for plant size where there seems to be more overlap than indicated by Reimer. In addition, I consider habitat, and cell shape to be important in separating these species. These characters are discussed under *O. fulvum* and summarized in Table 5.

5. *Orthodicranum strictum* Culmann, Bull. Soc. Bot. France 67: 201. 1920. (Based on type of *Dicranum strictum* Schleicher *ex* Mohr).

Dicranum strictum Schleicher *ex* Mohr, Crypt. Helv. Cent. MI. No. 26. 1806. *Hom. illeg., non Dicranum strictum* Smith, Fl. Brit. 3: 1218. 1804.

Type: *"Lectum in sylvis supra Mercles in Helvetia a Schleichero."* (Lectotype - G!)

Dicranum tauricum Sapehin, Bot. Jahrb. 105: 10. 1911. (Based on type of *Dicranum strictum* Schleicher *ex* Mohr).

Plants small, (0.5) 1.5-5.0 cm tall, in dense mats, light-green, growing on logs or living trees. Stems lightly tomentose, tomentum red to brown. Leaves when dry straight, erect and slightly imbricate, not undulate, similar when moist (2.5) 3.0-6.0 (7.5) mm long, narrowly lanceolate, tapering to a sharply acute tip when intact, tips usually broken off, tubulose or rounded, not keeled, abaxial and adaxial surface smooth, not papillose, margins entire, unistratose; costa narrow, (75) 90-120 (135) µm wide just above alar region, strongly excurrent, smooth on both surfaces, costa in median transverse-section showing 5 to 7 guide cells and no stereid bands, 1 or 2 rows of cells above and below guide cells with thickened walls and large lumens, the adaxial and abaxial layers of external cells not differentiated. Alar cells red to brown, thin-walled unistratose, not reaching costa, basal cells just above alar region rectangular, thin-walled, smooth (50) 65-110 (130) µm long, median cells short-rectangular to quadrate, thin-walled 30-80 (90) µm in fairly uniform rows, upper cells similar to median, 25-40 (50) µm long. Perichaetial leaves gradually tapering to a subulate tip.

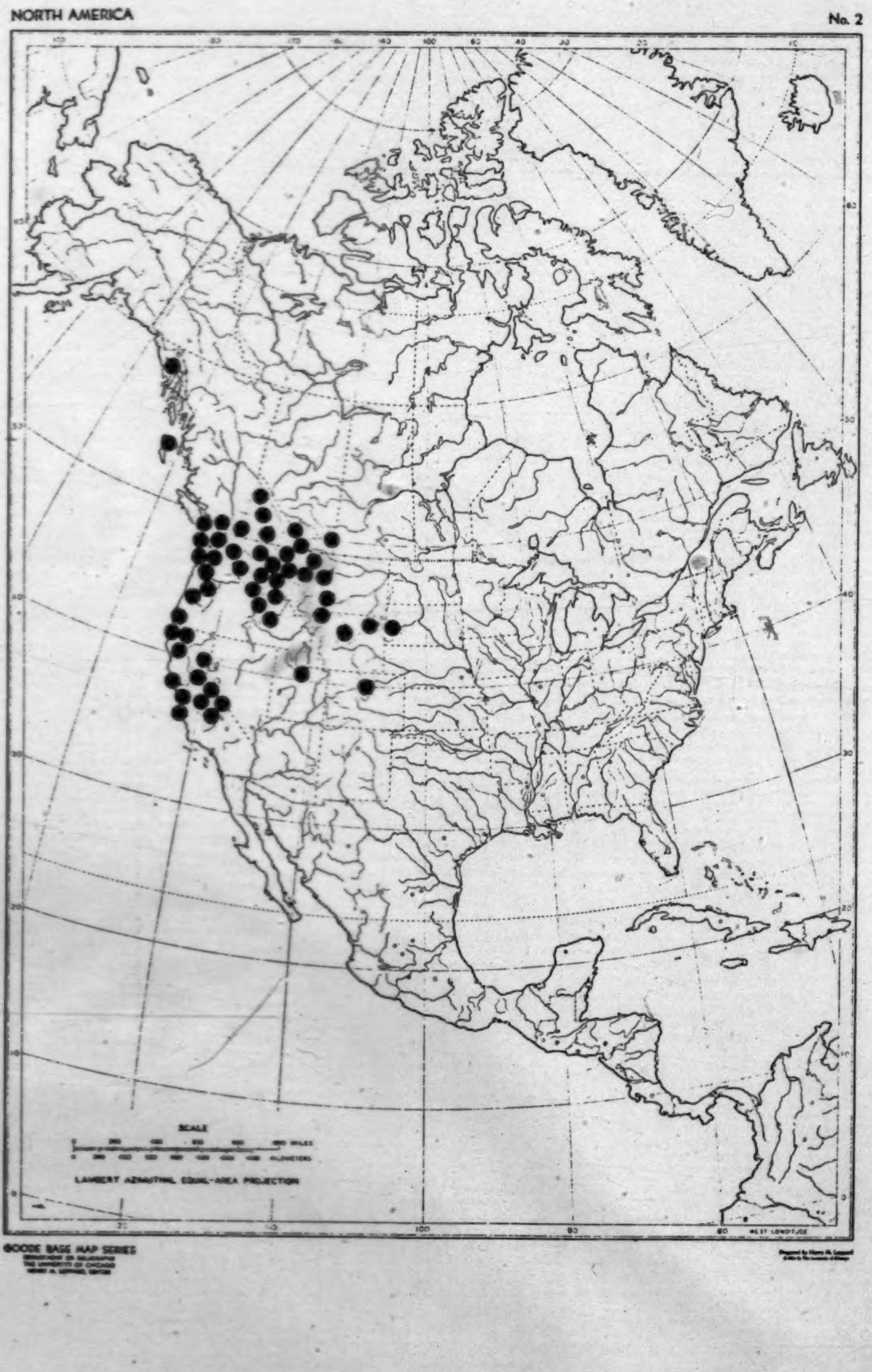
Dioicous, male plants slightly smaller than female ones. Monosetous, setae yellow to brown, 1.0 — 3.0 (3.5) cm long. Capsules light-to dark-brown, 1.5 — 2.5 mm long, erect, cylindric, smooth or slightly wrinkled, slightly constricted below mouth, neck short; exothecial cells rectangular, thin-walled; stomates few, 3 to 4 at base of capsule, 28-33 µm long; opercula rostrate, 1.0-1.5 mm long; annulus absent; peristome teeth red to orange, faintly vertically striate, about 0.5 mm long, (15) 20-40 µm wide at base, divided half way down into 2 segments; spores green to light-brown, 10-13 (16) µm, lightly papillose. Chromasome number, n=14 (12+2).

Habitat and Distribution (Fig. 22): *Orthodicranum strictum* is found in western North America, usually on logs or trunks of such coniferous species as *Pseudotsuga menziesii* (Mirb.) Franco and *Sequoia sempervirens* (D. Don) Endl. It is abundant along the coast from central British Columbia southward to central California where it also occurs in the *Sequoia gigantea* (Lindl.) Decne. forests of the Sierra Nevada Mountains. In the northwestern portion of its range it extends eastward through the Rocky Mountains into Waterton National Park and the Cypress Hills of Alberta. It also extends slightly down the eastern slope of the Rocky Mountains into western Montana and Colorado, reaching as far east as the Black Hills of South Dakota. Also, it has been collected in the southern tip of Alaska and it is found in Europe.

Selected Specimens Examined: EXSICCATI. Allen, Mosses Cascade Mts. Wash. 7 (DUKE, US, F, FH, NY, CANM). Grout, N. Am. Musci Perf. 131 (CAS, UC, F, FH, DUKE, NY, CANM). Holzinger, Musci Acroc. Bor. Amer. 32 (US, UC, F, FH, NY). Holtzinger, Musci Acroc. Bor. Amer. et Eur. 635 (UC, NY, CANM). Renauld and Cardot, Musci Amer. Sept 273 (CANM).

CANADA. Alberta: Turner Valley, Bird and Glenn 11829 (LAF). Cypress Hills, Lonepine campsite, Bird 4754 (CANM). British Columbia: Queen

FIGURE 22. The North American distribution of *Orthodicranum strictum* Culmann


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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WEST LONGITUDE
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Charlotte Is., W side of Botany Inlet, Schofield 37639 (SMS). Silverton, Grout 131 (CAS). Arrow Lake, Macoun, June 6, 1890 (NY). Agassiz, Macoun, April 6, 1889 (NY). Duncan, Flowers 7939 (COLO). 15.5 km W of Kimberley on Hw. 95A, Vitt 18121 (ALTA).

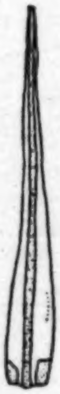
U.S.A. Alaska: Juneau, Mendenhall Valley, Worley 11729 (COLO). California: Del Norte Co., Gordon Mtn., Norris 7852 (CAS) Siskiyou Co., Salmon River, Norris 9192 (COLO). Mono Co., White Mtns., Mitchell, July 10, 1963 (UC). Calavaras Co., Calavaras Big Tree Grove, Koch 1663 (CAS). Trinity Co., Hayfork, Howe, June 11, 1896 (CAS). Nevada Co., Nevada, Tavares 6620 (UC). Tulare Co., Sequoia Nat. Park, Peterson 3242 (ALTA). Colorado: Boulder Co., Boulder Canyon, Weber B-5528 (COLO). Wallowa Co., Hermann B-11985 (COLO). Upper Gregory Canyon, Bowers 66-95 (SMS). Idaho: Idaho Co., Kooshia, Hermann 20202 (US). Natah Co., Moscow Mtn., Smith, Oct. 1, 1966 (ARIZ). Elmore Co., McFadden 19109 (SMS). Coeur d'Alene Nat. Forest, Mueggler 8M-31 (DUKE). Nez Pierce Co., Genesee, Schroeder M281 (LAF). Montana: Little Belt Mountains, Leiberg 782 (US). Sanders Co., Fishtrap Creek, Taylor 7062 (SMS). Missoula, Stickney 1046 (CAS). Flathead Co., Glacier Nat. Park, Hermann 22404 (CAS). Boulder Plateau, Leiberg 1489 (US). Oregon: Douglas Co., Crystal Springs, Redfearn 11653 (US). Umatilla Co., Pendleton, Hermann 18769 (CAS). Josephine Co., Caves Trail Camp, Mueller 6722 (UC). Corvallis, Gilbert 228 (F). South Dakota: Black Hills, Spearfish, Thompson 1892 (MIN). Utah: Utah Co., Mt. Timpanogos, Flowers 2961 (COLO).

Washington: Stevens Co., Flowers 9775 (COLO). Skamania Co., Weber 2851 (COLO). Kittatas Co., Lost Lake, Sharp B-40222 (COLO). Tacoma, Flett 990 (US). Springdale, Cooke 23368 (DUKE). Wyoming: Yellowstone Nat. Park, Knowlton, Aug. 3, 1888 (US). Johnson Co., Bighorn Nat. Forest, Weber *et al.* B46685 (COLO).

Orthodicranum strictum is sometimes confused with *O. viride* and *Dicranum fragilifolium* since all three species reproduce vegetatively by means of broken leaf tips that act as propagulae; therefore when sterile, their macroscopic appearance is remarkably similar and the common habitat of decaying logs or tree bases also complicates identification. When fertile, *Dicranum fragilfolium* is easily separated from the other two by its strongly curved capsules. Microscopically all three species are very distinct. *Orthodicranum strictum* has a narrow costa (1/7 to 1/5 width of leaf base), alar cells that do not reach the costa, and no stereid bands showing in costal transverse-section. *Dicranum fragilifolium* has a costa about 1/4 the width of the leaf base, alar cells that reach the costa, and two stereid bands showing in transverse section. *Orthodicranum viride* has a costa about 1/3 the width of the leaf base, alar cells that usually reach the costa, 2 stereid bands and short-rectangular median cells that extend to near the leaf base. The geographic range is also an important factor in determining morphologically confusing specimens. *Orthodicranum strictum* is found west of the Rocky Mountains from southern Alaska to central California and in southern Alberta, western Montana and the

FIGURE 23. *Orthodicranum strictum* Culmann

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)



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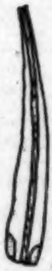

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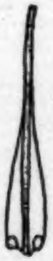

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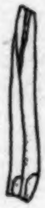

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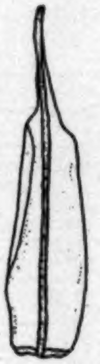

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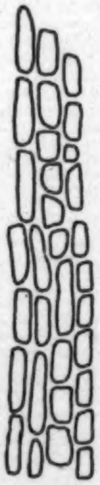

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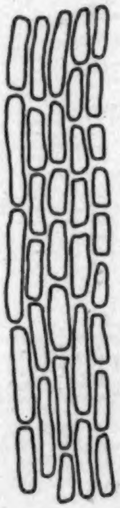

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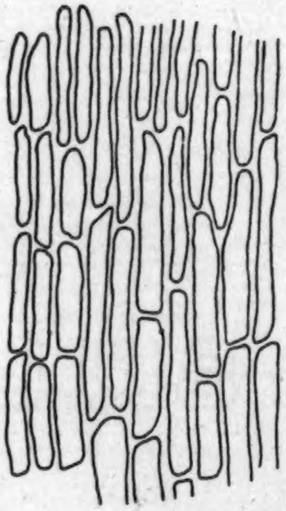

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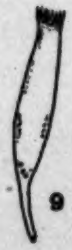

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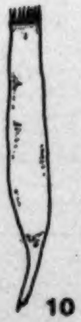

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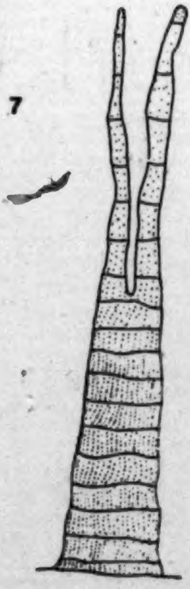

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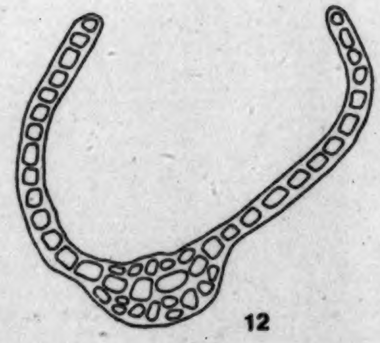

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Black Hills of South Dakota. *Dicranum fragilifolum* occurs in Canada, east of the Rocky Mountains and only overlaps the distribution of *O. strictum* in southwestern Alberta. Several collections from northern Alberta and Saskatchewan have been identified as *O. strictum*, but in all cases the specimens consisted of a mixture of sterile *Dicranum fragilifolium* and fertile *Orthodicranum flagellare* (which has erect capsules). *Orthodicranum viride* is restricted to eastern North America and its distribution does not overlap that of *O. strictum*.

Nomenclature: This species was originally described as *Dicranum strictum* by Schleicher in 1806; however, the name had been previously used by Smith (1804) in describing what is now a synonym of *Ceratodon purpureus* (Wijk *et al.*, 1962). Therefore, the name *Dicranum strictum* Schleicher is an illegitimate homonym. Sapehin used the name *Dicranum tauricum* in 1911 for this species and his name is the nomenclaturally correct one if the species is retained within the genus *Dicranum*.

Culmann (1920) was the first person to recognize this species in the genus *Orthodicranum* and he made the new combination *Orthodicranum strictum* (Schleicher) Culmann, using the illegitimate homonym as the basionym. According to article 72 of the ICBN (Stafleu *et al.*, 1972) Schleicher cannot be credited with the name and Culmann must be considered as using a new name instead of making a new combination. Therefore, the nomenclaturally correct name in the genus *Orthodicranum* is *Orthodicranum strictum* Culmann.

Dicranum Hedw. Spec. Musc. 126: 1801.

Lectotype: *D. scoparium* Hedw.

Cecalyphum P. Beauv., Mag. Enc. 5: 307. 1804. *nom. illeg. incl. lectotype gen. prior.*

Dicranodon Béheré, Musc. Rotham. 27. 1826. *nom. illeg. incl. gen. prior.*

Plants small to large, up to 15 cm tall, in loose to dense mats or tufts, occasionally as individuals mixed with other moss species. Stems erect, simple to sparsely branched, lightly to densely tomentose, tomentum white to brown. Leaves when dry straight, erect, or falcate-secund, sometimes crisped or twisted, when moist straight, erect, spreading, imbricate or rarely arching away from stem, smooth or undulate, fragile tips rarely present, sometimes papillose on abaxial surface; lamina unistratose or rarely bistratose near apex; apex acuminate, acute or rarely cucullate; margins plane, unistratose, bistratose, or rarely tristratose, entire, serrulate, serrate or dentate; costa narrow, usually 1/4 to 1/8 of leaf base width, subpercurrent to excurrent, smooth, toothed or lamellate on abaxial surface, smooth on adaxial surface; in median transverse-section showing 3 to 10 guide cells and two stereid bands (rarely one or none), one abaxial and one adaxial to the guide cells and extending into the leaf apex, abaxial and adaxial layer of external cells occasionally differentiated from stereids by larger lumens; alar cells always present, bistratose or with bistratose areas, inflated, thin- to thick-walled, dark in color, sometimes hyaline, seldom extending to costa, walls smooth or pitted; basal cells just above alar region, elongate to linear, 20-120 µm long, thin- to thick-walled, smooth or pitted, rarely similar to median cells; median cells quadrate to long-rectangular or occasionally triangular, 10-105 µm long, smooth to stongly pitted, corners sometimes rounded, occasionally arranged in uniform rows; upper cells quadrate to long-rectangular, 5-70 µm long, usually similar to median cells. Attenuated stem tips occasionally produced, 0.5-5.0 cm long, with short leaves 2.0-3.5 mm long, ovate to ovate-lanceolate, margins smooth to serrate. Perichaetial leaves usually shorter than stem leaves, emarginate, apiculate, abruptly narrowed or gradualy narrowed into a subulate tip. Perigonia ovate, about 1.5 mm long, in full sized male plants positioned slightly below the apex; antheridia club shaped, 0.3-0.7 mm long, 8 to 15 per perigonium, intermixed with filamentous paraphyses.

Dioicous, male plants dwarfed, positioned on tomentum or leaves of female plants, or of similar size and mixed with female plants or occasionally growing as separate populations. Monosetous or polysetous, setae extending well above leaves, yellow to brown. Capsules strongly curved to almost straight, ribbed or wrinkled, sometimes strumose, neck short to long; exothecial cells rectangular, 40-100 µm long, thin-or thick-walled; stomates in one row at base of capsule, 13-52 µm long; opercula conic with a short to long rostrum, 1.0-2.5 µm, smooth; peristome of 16 teeth inserted on capsule rim and dividid about half way to base into 2 or 3 segments, the outer surface vertically striate in lower 2/3 or more, usually papillose above; annulus absent or of one to three rows of enlarged, thick-walled, hyaline cells, persistent or fragmenting. Spores green to brown, 13 — 32 μm, smooth to papillose. Calyptrae cucullate and smooth. Chromosome numbers: n=8, 11, 12, 13 (12+1), 14 (12+2), 17 (12+5), and 24.

Habitat: Specimens of *Dicranum* are usually found growing on soil or humus, but may occasionally occur on other substrates. *Dicranum fragilifolium*, *D. fuscescens*, and *D. sulcatum* normally grow on wood (the former two usually on logs and the latter often on living coniferous trees), *D. condensatum* and *D. spurium* grow on sandy soil, and *D. leioneuron* and *D. undulatum* occur primarily in peatland habitats. Of the remaining species, almost half occur primarily in tundra habitats, and half occur on humus in more or less forested areas (Table 3).

Distribution: As a genus, *Dicranum* is found in all parts of North America except such arid regions as the deserts and prairies of the southern and southwestern United States. The most widespread is *D. scoparium*, which is found in almost all provinces and states as well as parts of Mexico, while the species with the most restricted distribution patterns are *D. leioneuron* and *D. amannii*. Both of these species occur in Europe, but in North America, the former is found only in the Maritime Provinces of Canada while the latter is found only in the northeastern High Arctic and the Yukon. Five other species and one variety also have limited patterns of distribution and are endemic to North America. These are *D. condensatum* of the southeastern United States, *D. ontariense* of the St. Lawrence River region, *D. pallidisetum* of northwestern United States and British Columbia, *D. rhabdocarpum* of the Rocky Mountains, *D. sulcatum* of the Pacific coast region and *D. brevifolium* var. *bistratosum* of the Canadian Rocky Mountains. The remaining species occur in Europe, and Asia and, in the case of *D. scoparium*, in Australia and New Zealand.

Taxonomy: I have divided the genus *Dicranum* into five sections based on both sporophytic and gametophytic similarities. The following synopsis distinguishes these sections and Table 6 lists the North American species found within each.

Synopsis of Sections of *Dicranum*

1. Upper leaf cells long, walls thin, lamellae or remnants of lamellae often present on abaxial costal surface .... section *Dicranum* Hedw.

1. Upper leaf cells short (or if long, with thick walls), lamellae or remnants of lamillae absent 2

    2. Upper leaf cells with thick walls (total distance between cells), walls as thick as lumens, capsules small (usually <2.5 mm long) .... section *Elongata* Hag.

    2. Upper leaf cells with thin walls, walls about 1/3 to 1/2 width of lumen, capsules larger (usually >3 mm long) 3

3. Median transverse-section showing stereids with large lumens, capsules with long necks ... section *Muehlenbeckia* Peterson

3. Median transverse-section showing stereids with small lumens, capsules with short necks 4

    4. Upper and median cells quadrate or rectangular, arranged in fairly uniform rows, leaves not undulate ... section *Fuscescentiformia* Kindb.

    4. Upper and median cells angular, slightly elongate or variously angled, loosely arranged in patterns not discernable as uniform rows, leaves undulate ... section *Spuria* B.S.G.

Section *Dicranum*: This is the easiest of the sections to distinguish, as all *Dicranum* species with long upper leaf cells, except *D. groenlandicum* which has very thick walls (Fig. 46-6), fall under this heading. Characters most important for distinguisning species within section *Dicranum* are the number of setae per perichaetium, the presence or absence of undulations on the lamina, the presence or absence of lamellae on the abaxial costal surface, and the strength of the stereid bands as seen in transverse-section.

Section *Elongata* Hag.: There are only two species in this section, which is distinguished by lamina cells that have walls as thick as or thicker than the cell lumens (Figs. 43-6, 46-6) and small capsules. The major characters for distinguishing the species are the length of the upper cells, the wall pitting, and the curvature of the capsule.

TABLE 6. The five sections recognized within the genus *Dicranum* and the North American species of each.

Dicranum	*Elongata*	*Fuscescentiformia*	*Muehlenbeckia*	*Spuria*
D. amanii Peterson	*D. elongatum* Schleich.	*D. fragilifolium* Lindb.	*D. brevifolium* Lindb. var. *brevifolium*	*D. acutifolium* (Lindb. & Arn.) C. Jens.
D. angustum Lindb.	*D. groenlandicum* Brid.	*D. fuscescens* Turn.	*D. brevifolium* var. *bistratosum* Ireland *ex* Peterson	*D. condensatum* Hedw.
D. leioneuron Lindb.		*D. pallidisetum* (Bailey) Ire.	*D. muehlenbeckii* B.S.G.	*D. ontariense* Peterson
D. majus Sm.		*D. sulcatum* Lindb.	*D. spadiceum* Zett.	*D. spurium* Hedw.
D. polysetum Sw.				*D. undulatum* Brid.
D. rhabdocarpum Sull.				
D. scoparium Hedw.				

Section *Fuscescentiformia* Kindb.: This section contains four species that have median and upper cells which are quadrate or rectangular in shape and are arranged in fairly straight rows. The leaves are never undulate and the costa has stereid cells with small lumens. The major characters for determining the species are the median costal transverse-section, the fragility of the leaf apex, and habitat.

Section *Muehlenbeckia* Peterson: This section consists of three species and one variety that were previously considered members of the section *Fuscescentiformia*; however, the nature of the stereid cells, which are different from those found in all other *Dicranum* sections, and the long capsule neck, suggests a separate group. The stereid cells when viewed in median transverse-section are seen to have lumens with a diameter about equal to the width of the cell wall (Fig. 13-2) while other Dicrana have stereids with lumens about half the diameter of the cell wall (Fig. 13-1). The taxa within the section are distinguished by leaf shape, layers of laminal cells near the apex, and costal width.

Section *Spuria* B.S.G.: This section contains all of the Dicrana that have short upper cells and undulate leaves. In addition, the median and upper cells are variously shaped, usually many are triangular or many angled and sometimes wider than long. The cells are not arranged in uniform rows. Within the section, species are distinguished by seta number, leaf and leaf apex shapes, and the arrangement of the median and upper leaf cells.

Section: *Fuscescentiformia* Kindb., Eur. N. Am. Bryin. 2: 187. 1897.

Lectotype: *Dicranum fuscescens* Turn.

Plants up to 10 cm tall. Leaves not undulate, falcate-secund to erect, apex acute, sometimes fragile; upper and median lamina cells rectangular to quadrate, usually arranged in uniform rows; median transverse-section of costa showing one row of guide cells and 2 stereid bands (bands absent in *D. pallidestum*), lumens of stereids small (<1/2 the wall thickness). Capsules curved, ribbed, usually strumose, neck short; annulus present.

6. *Dicranum fragilifolium* Lindb., Bot. Not. 146. 1857.

Types: "... Juli 1856 ... Pitea Lappmark ..." (Syntype-H!); "... Gotland ... N.C. Kindberg" (Syntype not seen); "... Lappland ... Swartz ... " (Syntype not seen).

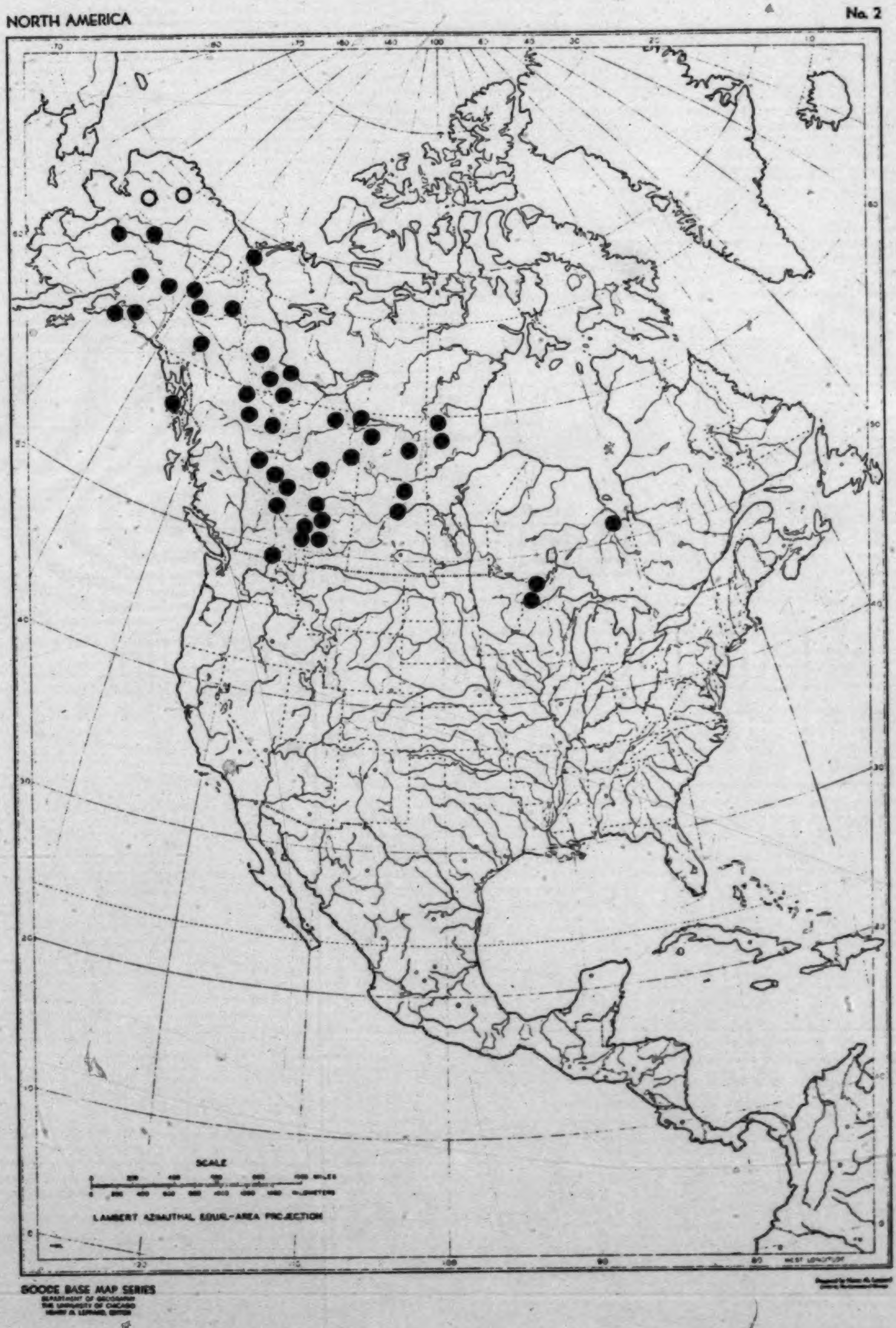
Orthodicranum fragilifolium (Lindb.) Podp., Consp. 152. 1954.

Plants small, up to 4.5 cm tall, in loose to dense mats on decaying wood or humus. Stems moderately to densely tomentose, tomentum dark-brown to red. Leaves when dry erect or slightly twisted near the tip, when moist erect and stiff, not undulate, (2.0) 4.0-6.0 (8.5) mm long, lanceolate, tapering to a subulate tip, upper portions often fragile and broken off, slightly tubulose in upper half, concave below, not keeled above or below, abaxial and adaxial surface smooth; margins entire or rarely slightly serrate near tip, unistratose; costa narrow, 95-125 (140) µm wide just above alar region, excurrent to percurrent, smooth, costa in median transverse-section showing 6 to 8 guide cells and 2 stereid bands, both bands extending into upper 1/4 of leaf, each band composed of 2 to 3 rows of thick-walled cells with small lumens, the adaxial and abaxial alyers of external cells not differentiated from stereid cells; alar cells brown to red-brown, thin-walled, bistratose, extending to the costa; basal cells just above alar region rectangular, usually thick-walled, slightly pitted, (35) 40-60 (75) µm long; median cells short-rectangular, thin-walled, 20-30 (45) µm long and arranged in fairly uniform rows; upper cells short-rectangular, thin-walled, smooth, 12-20 (26) µm long. Perichaetial leaves shorter than stem leaves and abruptly narrowing to a long, subulate tip.

Dioicous, male plants similar to female plants, Monosetous, setae brown, 1.0-2.5 (2.8) cm long. Capsules light-to dark-brown (1.2) 1.5-2.5 cm long, curved, ribbed, sometimes slightly strumose, neck short; exothecial cells rectangular, thin- or thick-walled, slightly pitted; stomates few, in one row at base of capsule, 24-28 µm long; opercula rostrate, 1.2-1.6 mm long; annulus of 2 to 3 rows of large, thick-walled, hyaline cells; peristome teeth red to brown, vertically striate, about 0.5 mm long, (60) 75-95 µm wide at base, divided 1/2 way down into 2 segments; spores green to brown, smooth or very lightly papillose, 16-23 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 24): *Dicranum fragilifolium* is generally found on decaying wood and may occasionally occur on humus. It

FIGURE 24. The North American distribution of *Dicranum fragilifolium* Lindb.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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
WEST LONGITUDE

is distributed in the boreal region from Alberta east to eastern Ontario, northern Michigan, south to Montana and Minnesota and north into the Yukon and Northwest Territories. It is not abundant except in the area east of the Rocky Mountains and west of the Canadian shield. In Alberta, *D. fragilifolium* is the most common member of the genus to be found in *Populus tremuloides* or mixed *Populus tremuloides-Picea glauca* forests and usually grows on *Populus* logs although it sometimes occurs on *Picea* logs. *Orthodicranum strictum* has been erronously reported from central Alberta (Moss and Turner, 1961), Manitoba (Ritchie, 1956), and Saskatchewan (Lawton, 1971) with the reports based upon sterile *D. fragilifolium* intermixed with fertile *D. flagellare* which produces erect capsules. At first glance, one sees only erect capsules and broken leaves, character states that determine *O. strictum*; however, the erect capsules are not attached to the plants that have the broken leaves. Distributional overlap between these two species does occur in southwestern Alberta and microscopic examination is necessary for positive determinations.

Selected Specimens Examined: EXSICCATI. Drummond, Musci Amer. (Rocky Mtns.) 92 as *D. elongatum* var. *minor* (NY, CANM, FH).

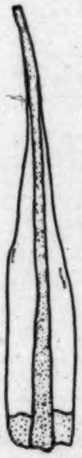
CANADA. Alberta. Jumping Pound Creek, Macoun 109 (US). Ma-Me-O Beach, Turner 9794 (ALTA). Wood Buffalo National Park, Raup 2027 (MICH). Lesser Slave Lake District, Brinkman 4161 (TENN). Camrose, 12.8 km SW of city, Bird 6847 (UAC). Bow River watershed, Wildcat

Hills, Bird 9933 (UAC). Sherman Meadows, Two Lakes campground, 54°17'N, [illegible]'W, Peterson 1199 (ATLA). Willmore Wilderness Area, 53°28'N, 118°22'W, Peterson 3415 (ALTA). British Columbia: Robson, MacFadden 3649 (TENN). Aleza Lake, 1 km W of Aleza Lake Ranger Station, Peterson 3198 (ALTA). Alaska Hw., mile 225 N of Ft. St. John, Peterson 3146 (ALTA). Liard Hot Springs, 126°08'W, 59°26'N, Peterson 3087 (ALTA). Manitoba: Horshoe Lake, 57°43'N, 101°15'W, Scotter 3610 (CANM). Kasmere, 59°34'N, 101°10'W, Scotter 3412 (UAC). Ontario. Moose Factory, Lepage 13831 (US). Hawley Lake, 0.8 km N of Narrows, Williams 1746 (MICH). Saskatchewan: Prince Albert National Park, Hand 60-238 (UAC). LaRonge, LaRonge Lake, Guccion, Aug. 10, 1957 (SMS). Northwest Territories: Nahanni River Region, 61°28'N, 125°51'W, Scotter 13476 (CANM). Mackenzie Lowlands, Laird River Valley, Jeffrey 23 (CANM). Flat River, 61°28'N, 125°51'W, Scotter 13476 (CANM). Yukon Territory: Aklavik, Krajina *et al.* 6307013 (DUKE). Little Salmon River, Willaims 535 (F). Dawson, Williams 424 (F).

U.S.A. Alaska: Valdez, along Lowe River, Hermann 21723 (CANM). Galena, between Galena and Kobuykak, Peive M21a (MICH). Central Alaska Range, 63°44'N, 149°30'W, Walurhaftig 2a (MICH). Bethil, Butyan 9338 (DUKE). Evans Is., Port San Juan, Eyerdam 5203 (MICH). Michigan: Keweenaw Co., Isle Royale; Baziun 9386 (MICH). Isle Royal, Smithwick Islands, Povah 500 (TENN). Minnesota: Cook Co., Grand Marais, Holzinger, July 31, 1902 (DUKE).

FIGURE 25. *Dicranum fragilifolium* Lindb.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)
13	Upper transverse-section (280x)
14	Basal transverse-section (280x)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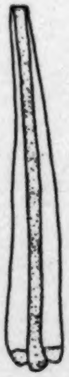
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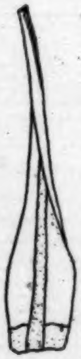
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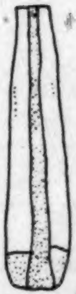
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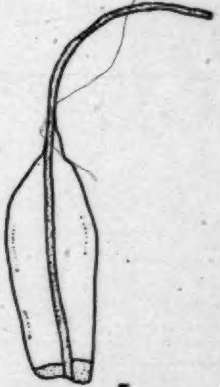
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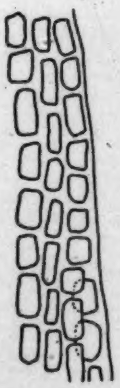
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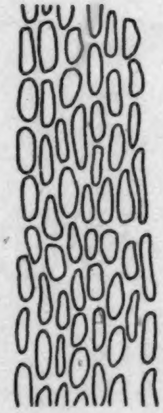
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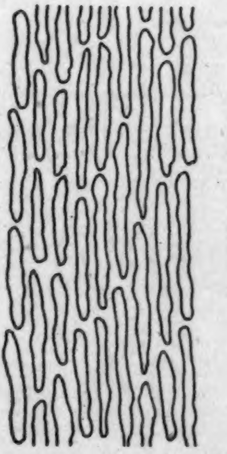
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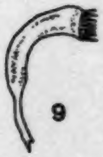
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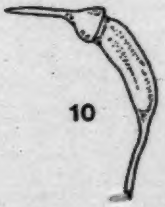
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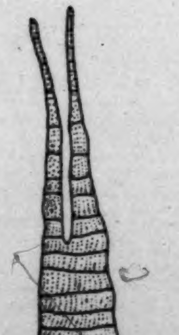
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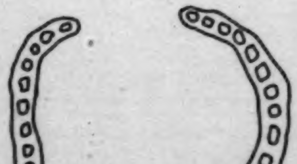
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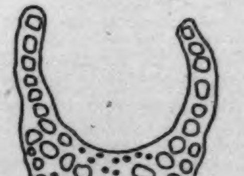
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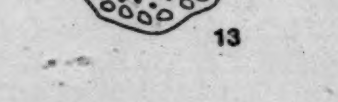
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Dicranum fragilifolium is the only member of the genus that has broken leaf tips, and therefore should not be confused with any other *Dicranum* species. In the sterile condition, it may be confused with *Orthodicranum strictum* or occasionally *O. viride*; however, this should only be a problem in the areas where distributions overlap. The difinitive character in separating *D. fragilifolium* from *O. strictum* is the costa transverse-section with the former having 2 to 3 rows of stereid cells in median section (Fig. 25-12) while the latter lacks stereids (Fig. 23-12). Also, the alar cells of *D. fragilifolium* always extend to the costa while those of *O. strictum* do not. In the eastern portion of *D. fragilifolium*'s range where overlap occurs with *O. viride*, it is easy to separate sterile specimens of the two on the width of the costa since the latter has a basal costa width seldom less than 1/3 that of the leaf and the costa of the former seldom exceeds 1/5 of the width of the leaf base.

7. *Dicranum fuscescens* Turn., Musc. Hib. 60. 1804.

Type: "*... mox in rupibus circa lacum Lough Bray dictum, legit D. Stokes.*" (Holotype-BM!)

Dicranum congestum Brid., Musc. Recent. Suppl. 1: 176. 1806.

Type: "*In Jurae sylvis detexit amicus Dejean ...*" (Holotype-B!)

Dicranum leucobasis C. Müll. and Kindb. *in* Macoun et Kindb., Cat. Can. Pl. 6: 30. 1892.

Types: "On basis of trees in woods west of Columbia River at Revelstoke, B.C., May 6, 1890; and in Rogers Pass, Selkirk Mountains. Coll. Macoun." (Syntypes-CANM! S!).

Dicranum trachyphyllum Ren. et Card., Bot. Gaz. 22: 48. 1896.

Type: "Newfoundland, Leading Pickles and Hermitage Bay. Coll. Rev. A.C. Waghorne, 1893 and 1895". (Type not seen) *fide* Williams, 1913.

Dicranum camptophyllum Kindb., Eur. and North Amer. Bryin. 193 1897.

Type: "Northern Labrador, 1896". (Lectotype-S!, Isotype-CANM!).

Dicranum camptophyllum Kindb. var. *poriferum* Kindb. *in* Macoun et Kindb., Cat. Can. Pl. 7: 198. 1902.

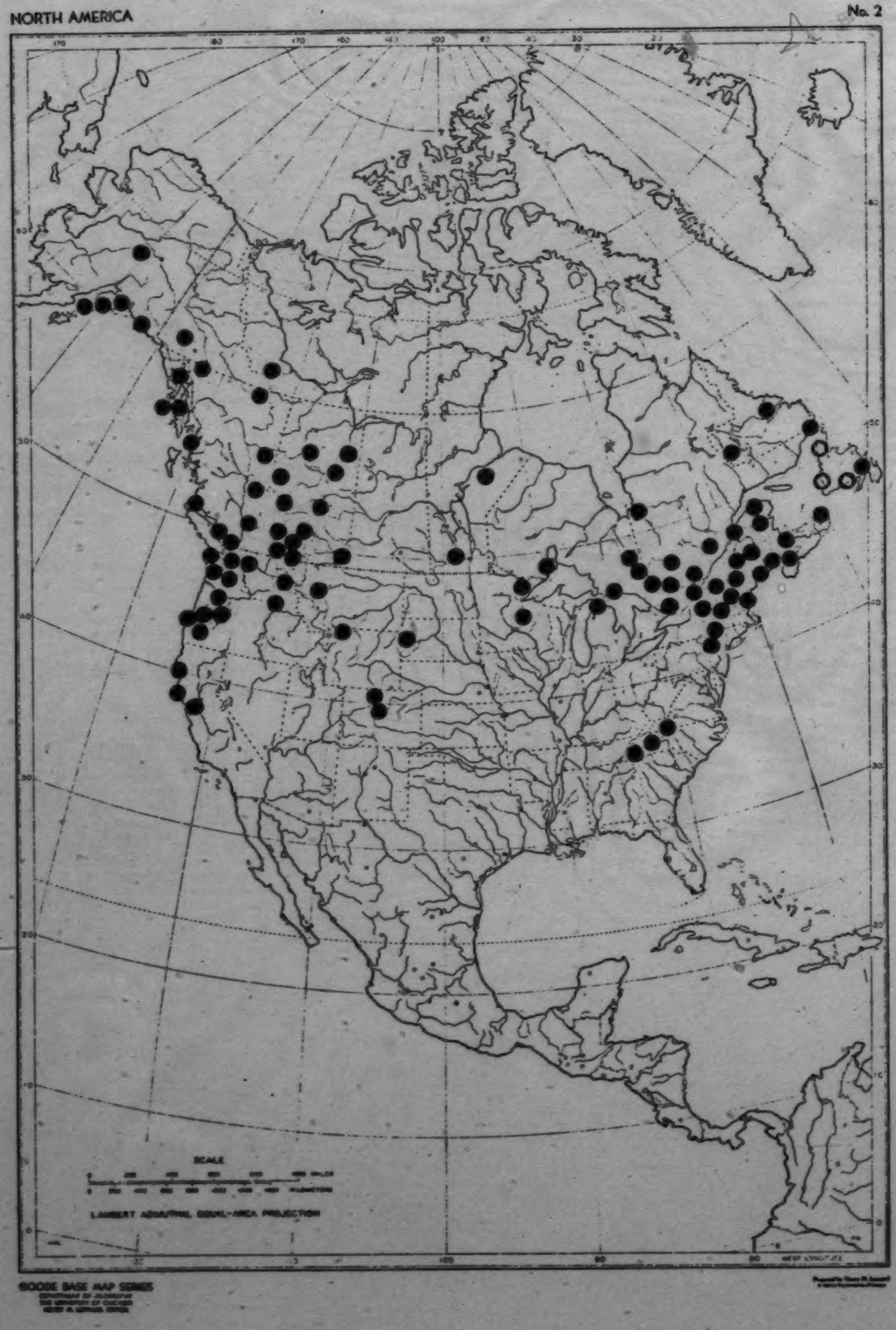
Type: "Elbow River, Alberta" (Lectotype-S!, Isotype-CANM!).

Plants in dense mats or small tufts, up to 8 cm tall, light-green, growing on logs or occasionally on humus. Stems moderately tomentose, tomentum brownish. Leaves when dry falcate-secund to crisped, when moist falcate-secund, not undulate, 4-7 (8) mm long, long lanceolate, tapering to a sharply acute tip, keeled in upper 1/2, smooth or slightly papillose on upper abaxial surface; margins moderately to strongly serrate and bistratose in upper half, occasionally unistratose in spots; costa narrow, 115-135 µm wide just above alar region, percurrent or slightly excurrent, toothed on upper abaxial surface, costa in median transverse-section showing 7 to 9 guide cells and 2 well developed stereid bands, both bands extending well into the apex, each band composed of 2 or 3 cell layers, abaxial layer of external cells well differentiated from stereids by large lumens, adaxial layer not differentiated; alar cells brown,bistratose, thin-walled, not reaching costa; basal cells above alar region elongate-rectangular, to 30-50 (65) μm long, not pitted, thick-or thin-walled; median cells short, rectangular to quadrate, in regular rows thick-walled, 15-25 (40) μm long, upper cells similar, slightly more irregular. Perichaetial leaves shorter than stem leaves, innermost ones abruptly narrowed to a subulate tip.

Dioicous, male plants similar to, or slightly smaller, than female plants. Monosetous, setae brown to yellow, 1.2-2.5 cm long. Capsules light-brown, 1.5-3.0 mm long, curved, ribbed, strumose, neck short; exothecial cells rectangular or irregularly angled, thick-walled, walls pitted; stomates in one row at base of capsule, 28-30 μm; opercula rostrate, 1.0-1.8 mm long; annulus of 1 to 2 rows of large, thick-walled, hyaline cells; peristome teeth orange to red, vertically striate, about 0.5 mm long, 75-90 μm wide at base, divided 1/2 way down into 2 segments; spores green to brown, papillose 16 - 24 μm. Chromosome number n=8, n=12.

Habitat and Distribution (Fig. 26): *Dicranum fuscescens* is a forest species usually found growing on such angiospermous logs as *Populus tremuloides*; however, it occasionally grows on coniferous logs or humus. It is not found in either the prairie regions or the tundra regions of the north except where isolated forest areas exist. The

FIGURE 26. The North American distribution of *Dicranum fuscescens* Turn.


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

species is circumpolar in distribution and is found in forested areas of North America from southern Alaska to central California and Colorado; across the boreal forest in Canada to Newfoundland and south in the deciduous forests through Michigan to Tennessee and North Carolina.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 472 (DUKE, NY, CANM). Drummond, Musci Amer. (Rocky Mtns.) 82 (F, CANM). Grout, N. Amer. Musci Perf. 259 (CAS, F, COLO, CANM, DUKE, FH), 40 (COLO). Grout, Hand-Lens Mosses 26 (DUKE). Holzinger, Musci Acroc. Bor. Amer. 486 (DUKE, CANM). Macoun, Can. Musci 39 (CANM, UC) 40 (CANM, UC, FH). Sull. and Lesq., Musci Bor. Amer. ed. I 64 (DUKE, FH), ed. II 80 (FH). Renauld and Cardot, Musci Amer. Sept. 206 (FH). Gray and Sullivant, Musci Allegh. 157, 158 (NY, FH).

CANADA. *Alberta*: Mountain Park Area, Whitehorse Creek campground, *Peterson 806* (ALTA). Battle Lake, just W of Pigeon Lake, *Peterson 1149* (ALTA). Rocky Mtn. House, 48 km S of town, *Peterson 3287* (ALTA). Two Lakes Region, 110 km S of Wapiti River, *Peterson 1252* (ALTA). Swan Hills, *Vitt 3943* (ALTA). *British Columbia*: Liard Hot Springs, 126°08'W, 59°25'N, *Peterson 3085* (ALTA). Bouron Lake, *Schofield 39251* (UBC). Indian Cove, Cape Caution, *Schofield 41098* (UBC). Alberta Canyon, *Macoun 96* (CANM). New Westminister, *Hill 585* (DUKE). Wilmer, *Grout 259* (CAS). *New Brunswick*: Albert Co., Fundy National Park, *Ireland 11596* (CANM). Restigouche Co., *Ireland 14371* (CANM). Charlotte Co., St. Andrews, *Ireland 13305* (CANM). *Newfoundland*:

Labrador, L'Anse-au-Clair, Waghorne, July 5, 1896 (MIN). Hodges Cove, near Random, Waghorne June 26, 1895 (MIN). Nova Scotia: Anapolis Co., Kejimkijik National Park, Ireland 12435 (CANM). Victoria Co., Cape Breton Highlands National Park, Ireland 11777 (DUKE). Ontario: Thunder Bay District, near Marathon, Schofield 27614 (DUKE). Timishaming Co., 20.8 km S of Ramore, Yuncher and Yuncher 5515 (DUKE). Quebec: Gatineau Park, Luskville Falls, Peterson 2382 (ALTA). Montcalm Co., Chutes Croches, Hermann 165933 (DUKE). Mt. Tremblant Park, Flowers 5837 (COLO). Yukon Territory: Lake Lindeman, Williams 536 (F). Kathleen Lakes, 60°37'N, 137°15'W, Scotter 18205 (C).

U.S.A. Alaska: Knight Is., Thum Bay, Eyerdam 610 (UC). Kuire Is., Washington Bay, Eyerdam 5402 (DUKE). Bear Glacier, Viereck 2110 (LAF). California: Marin Co., Mt. Tamalpais, Howell H276 (CAS). Humboldt Co., Eureka, Howe 971 (CAS). Sonoma Co., Koch 545 (COLO). Colorado: Black Head Peak, Grout 162 (F). Larimer Co., Rocky Mtn. National Park, Keiner 9279 (COLO). Idaho: Nez Pierce Co., Henderson June 1894 (F). Shoshone Co., Wallce, Flowers 7516 (COLO). Maine: Piscataquis Co., Mt. Katahdin, Crane 582 (DUKE). Oxford Co., Richards 6051 (DUKE). Hancock Co., Sorrento, Clebsch Aug. 11, 1951 (TENN). Norway, Bacon 501 (COLO). Michigan: Big Stone Bay, Nichols 379 (MICH). Isle Royale, Tonkin Bay, Stuntz and Allen 777 (MICH). Minnesota: Cook Co., Olsen B9492 (COLO). Montana: Flathead Co., Avalanch Lake Trail, Hermann 17961 (CAS). Lake Co., Flathead Lake, Millar, Aug. 1967 (COLO). New Hampshire: Grafton, Hutchinson, Oct., 1947 (DUKE).

New York: Whiteface, Britton Sept. 21, 1896 (NY). Hunter Mtn., Haring Oct. 19, 1935 (DUKE). North Carolina: Jackson Co., Richland Balsam Mtn., Anderson 10779 (DUKE). Grandfather Mtn., Schallert M-88 (DUKE). Yancy Co., Anderson and Jones 9449 (DUKE). Oregon: Multnomah Co., Larch Mtn., Redfearn 11560 (SMS). Umpqua National Forest, Redfearn 11643 (SMS). Clachamas Co., Mt. Hood, Hermann 18711 (CAS). Corvallis, Gilbert 233 (F). Pennsylvania: Monroe Co., Pocono Mtn., James 1869 (TENN). Tennessee: Mt. LeConte, Anderson 20828 (DUKE). Vermont: Newfane Hill, Hohub Aug. 1943 (DUKE). Stratton, Wynne, 1894 (DUKE). Virginia: White Top Mtn., Vale and Britton May 29, 1892 (UC). Washington: Olympic Hot Springs, Smith 2163 (SMS). Snoquami Pass, Reed July 25, 1896 (UC). Snohomish Co., near Index, Savage *et al.* July 1898 (F). Wisconsin: St. Croix Falls, Fletcher Nov. 15, 1953 (MIN). Wyoming: Yellowstone National Park, Firehole River Canyon, Welch 16493 (MIN).

Dicranum fuscescens is a name often applied to many different Dicrana that have short upper leaf cells. I have found as many as six different species filed under this name in one herbarium and virtually all members of the genus, except *D. polysetum* and *D. majus*, have had specimens named *D. fuscescens* at one time or another. Even though many species have been named *D. fuscescens* (promoting a poor understanding of the species) it is still quite distinct and should not be confused with others. It is sometimes difficult to separate from its close relative, *D.*

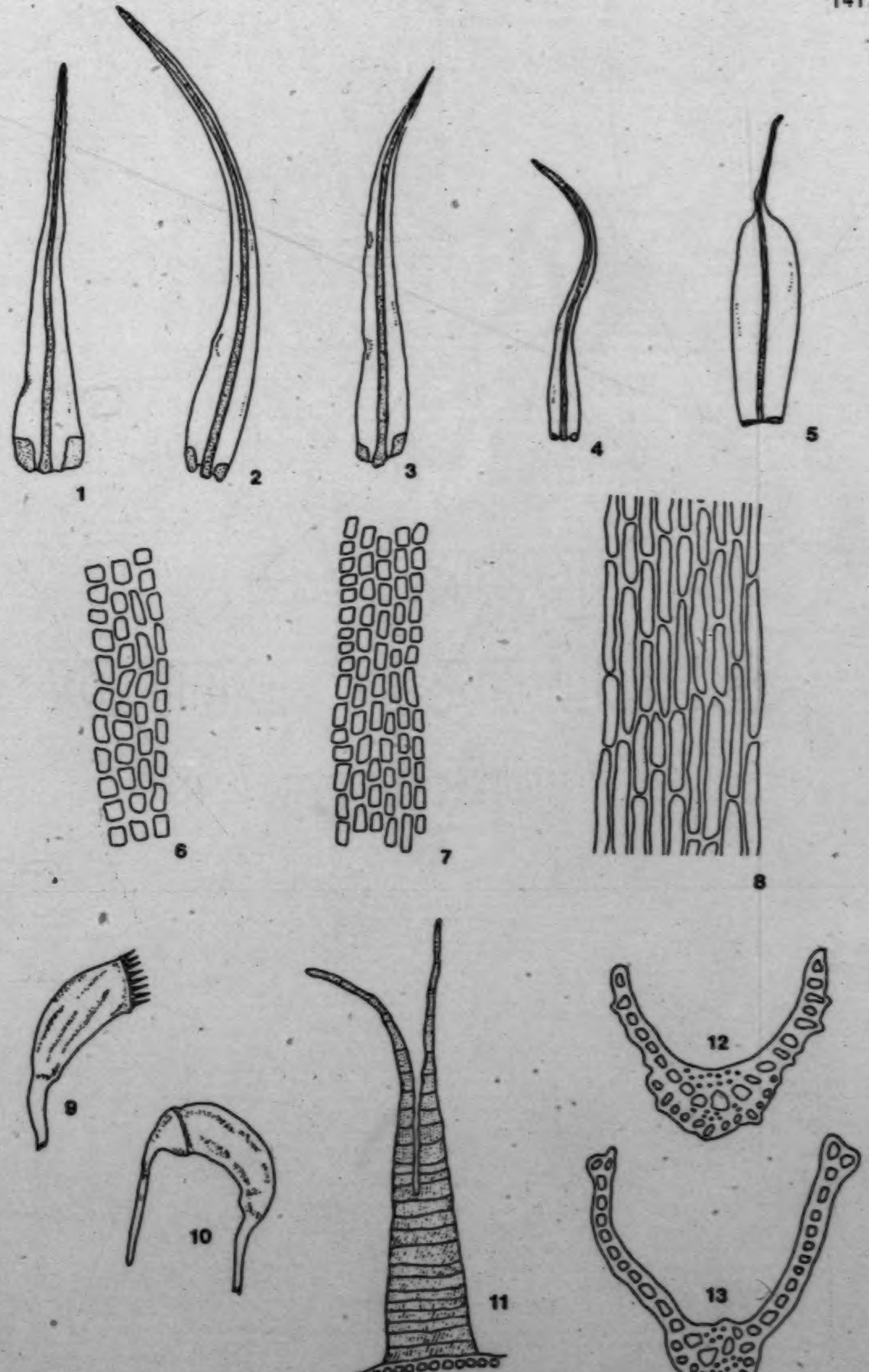
sulcatum (see discussion under *D. sulcatum*) and several other species that are more distantly related. These species (*D. acutifolium*, *D. brevifolium*, *D. pallidisetum*, *D. condensatum*, and *Orthodicranum fulvum*) have short upper leaf cells (majority of cells <4:1 in length/width ratio) and must be distinguished on characters such as costa width and transverse-section, habitat, and arrangement of the median cells. *Orthodicranum fulvum* has a wide costa (>1/3 width of leaf base) compared to *D. fuscescens* (about 1/5 of leaf base) and grows on rock. *Dicranum condensatum* grows on sandy soil and has strongly twisted leaves. *Dicranum acutifolium* often has some median cells that are longer (about 3:1 in length/width ratio), more angled and much more irregularly arranged (Fig. 53-8) than those of *D. fuscescens* (Fig. 27-7). *Dicranum pallidisetum* is separated by costal transverse-section; it lacks stereid bands (Fig. 32-12) in the upper half of the leaf.

Dicranum brevifolium and its var. *bistratosum* are two taxa not recognized by Crum *et al.* (1973) and often referred to as *D. fuscescens*; however, they are more closely related to *D. muehlenbeckii*. The median cells of *D. fuscescens* are quadrate with angular corners (Fig. 27-7) while *D. brevifolium* has quadrate cells with round corners (Fig. 39-7). There is also a major difference in the appearance of the stereids in transverse-section, with those of *D. fuscescens* having very small lumens (Fig. 13-1) as opposed to large lumens in *D. brevifolium*. (Fig. 13-2).

Dicranum fuscescens, like the remainder of the genus, normally has

FIGURE 27. *Dicranum fuscescens* Turn.

1-4 Stem leaves (14x)
5 Perichaetial leaf (14x)
6 Upper laminal cells (280x)
7 Median laminal cells (280x)
8 Basal laminal cells (280x)
9, 10 Capsules (10x)
11 Peristome tooth (180x)
12 Upper transverse-section (280x)
13 Median transverse-section (280x)



a chromosome compliment of n=12, however, counts of n=8 have been made (Anderson, *pers. comm.*). The n=8 material, which was collected in North Carolina, does not differ morphologically from the more common n=12 material except for slightly smaller guard cells. In the specimens examined (5 capsules) guard cells on the n=8 material ranged from 28 — 31 µm in length while those of the n=12 material ranged from 35- 39 µm. This difference suggests a quantitative character that could be used to separate different chromosome races in a manner sometimes used in vascular plants (Löve and Löve, 1975; Stebbins, 1971), but unfortunately, not enough material was available to provide a statistically sound analysis. It is possible that cytological studies in this group will eventually lead to the taxonomic recognition of the two chromasome races.

8. *Dicranum sulcatum* Kindb. *in* Macoun, Bull. Tor. Bot. Cl. 17: 87. 1890.

Types: "Victoria, Vancouver Island, 1887; quite common between Burrad Inlet and the Gold Range, B.C., 1889." (Lectotype - May 2, 1887, "Vancouver Is."-S!; Syntype - "July 1887, Vancouver Is."-CANM!)

Dicranum crispulum C. Müll. et Kindb. *in* Macoun et Kindb. Cat. Can. Pl. 6: 27. 1892.

Types: "On logs in woods at Comox, Vancouver Island, May 2, 1887." (Syntype-CANM!). "On logs in woods, Albert Cañon, May 29, 1890." (Lectotype-S!, Isosyntype-CANM!).

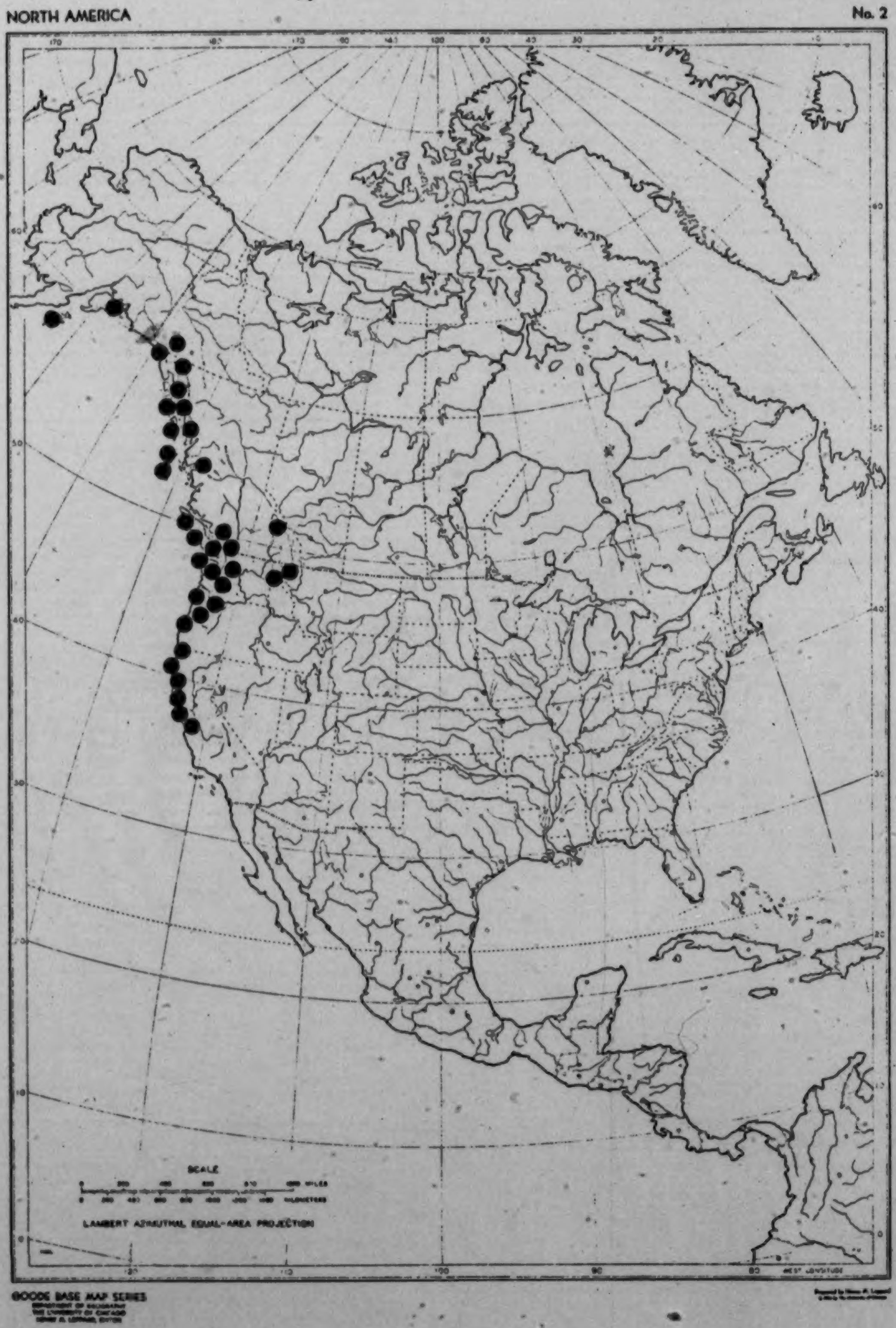
Plants in dense to loose tufts, up to 10 cm tall, dark-green, growing on decaying wood, living trees or rarely on humus. Stems moderately tomentose, tomentum light- to dark-brown. Leaves when dry falcate-secund with twisted tips, when moist falcate-secund, not undulate, (5) 6-9 mm long, lanceolate, tapering to a sharply acute tip, strongly keeled in the upper 2/3, papillose or rarely smooth on upper abaxial surface; margins strongly serrate and bistratose in upper 1/2 of leaf, rarely unistratose in spots; costa wide, 150-180 (195) µm wide just above alar region, usually strongly excurrent, rarely short-excurrent, toothed on upper abaxial surface, costa in median transverse-section showing 6 to 8 guide cells and two well developed stereid bands, both extending well into the apex, each band composed of 3 to 4 layers of cells with very small lumens, abaxial layer of external cells well differentiated from stereids by large lumens and often projecting as teeth on surface, adaxial layer not differentiated; alar cells brown, bistratose, thin-walled, not reaching costa, basal cells above alar region elongate-rectangular, up to 65 µm long, rarely pitted, thick- or thin-walled, median cells short, quadrate to rectangular, in very regular rows, thick-walled, 10-16 (22) µm long, cells of tip similar to median. Perichaetial leaves shorter than stem leaves, innermost ones abruptly narrowed to a subulate tip.

Dioicous, male plants similar to female plants. Monosetous, setae brown, 1.2-2.5 (3.5) cm long. Capsules light-brown to dark-brown, 1.5-3.0 mm long, curved, ribbed, strumose, neck short; exothecial cells irregular, thin- or thick-walled, pitted; stomates in one row at base of capsule, 30-35 µm; opercula rostrate (1.2) 1.5-2.0 mm long; annulus of 1 to 2 rows of large, thick-walled, hyaline cells; peristome teeth red to orange, vertically striate, 0.3 – 0.5 mm long, 75-90 (115) µm wide at base, divided half way down into 2 or rarely 3 segments; spores green to light-brown, thick-walled, papillose, 13-20 (23) µm. Chromosome number unknown.

Habitat and Distribution (Fig. 28): *Dicranum sulcatum* is endemic to the west coastal regions of North America, ranging from southern Alaska southward into the central coastal area of California. It has been collected inland as far as northern Idaho and the northwest corner of Montana but it does not extend east of the Rocky Mountains. Typically specimens are found growing in damp, shaded forests, on trunks of living trees such as *Sequoia sempervirens* and *Pseudotsuga menziesii* or occasionally on logs or stumps of these or other coniferous species. It rarely grows on angiospermous trees or logs but may be found occasionally growing on humus. *Dicranum sulcatum* is apparently restricted to areas where moist coastal forests exist. Its southern distributional limits correspond closely to that of *Sequoia sempervirens* and the northern limits are close to that of *Picea sitchensis*, another coastal coniferous tree.

Selected Specimens Examined: EXSICCATI. Macoun, Can. Musci 406 (US, UC). Holzinger, Musci Acroc. Bor. Amer. 33 as *D. congestum*

FIGURE 28. The known distribution of *Dicranum sulcatum* Kindb.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(UC, DUKE, MIN). Holzinger, Musci Acroc. Bor. Amer. et Eur. 610 as *D. congestum* (DUKE). Grout, N. Amer. Musci Perf. 259 as *D. fuscescens* (F, DUKE, FH). Renauld and Cardot, Musci Amer. Sept. 8 as *D. fuscescens* (FH).

CANADA. British Columbia: Queen Charlotte Is., Graham Is., Brent Creek, Schofield 30092 (ALTA). Queen Charlotte Is., Moresby Is., Upper Victoria Lake, Schofield 30840 (ALTA). Saltspring Is., Boas 227 (DUKE). Vancouver Is., Long Beach, Wade, June 1964 (DUKE). Vancouver Is., Mt. Arrowsmith Trail, Howell Aug. 1, 1931 (UC). Haney, McClintlock June 18, 1949 (CAS). Manning Prov. Park, Flowers 9523 (COLO).

U.S.A. Alaska. Metkof Is., Petersbury, Worley and Schofield 8666 (DUKE). Etolin Is., Worley and Hamilton 8271 (DUKE). San Juan Bautistia Is., Worley and Hamilton 7176 (DUKE). Douglas Is., Juneau Quadrangle, Hermann 22142 (DUKE). Sitka, Canby 463 (US). Haines, Worley 12196 (SMS). California: Del Norte Co., near Gordon Mtn., Norris 7843 (HSC). San Mateo Co., Howe 69 (UC). Orick, Eastwood 890 (CAS). Eureka, Eastwood 4561 (CAS). Humboldt Co., Samoa Penn., Franch Feb. 1970 (UC). Idaho: Bonner Co., Hanna's Flat, W of Priest Lake, Peterson 1104 (ALTA). Montana: Glacier National Park, McDonald Creek, Imshaug 7954 (CANM). Oregon: Multnomah Co., Larch Mtn., Redfearn 11571 (SMS). Coos Co., Coos Head, Dotz Dec. 10, 1941 (F). Washington: Lewis Co., Packwood, Smith Oct. 22, 1966 (ARIZ). Mt. Angeles, Hardhill 238 (SMS). Anacortes, Jackson Nov. 1930 (CAS). Olympia, Herre Aug. 7, 1954 (CAS). Seattle, Bailey Jan. 1903 (UC).

Dicranum sulcatum was described by Kindberg in 1890 from specimens collected on Vancouver Island, British Columbia by John Macoun. His description, although brief, included diagnostic features such as the deeply ribbed capsules and the wide, excurrent costa. Although Kindberg and Macoun adequately described this species it is generally regarded as a synonym of *D. fuscescens*. This is undoubtably due to the fact that Macoun and Kindberg have described innumerable new bryophyte species of which very few are considered valid. Most of their taxa are included as synonyms of previously established ones. In the case of *D. sulcatum*, even Kindberg in the original description (Macoun, 1890a) considered it very close to *D. fuscescens* and, as a result, it was treated as a synonym of *D. fuscescens* by Williams (1913). It has not been treated at any taxonomic level since, even though it is actually quite distinct and easily separated from *D. fuscescens* on the character states cited in the original description.

The characters that can be used to distinguish *D. sulcatum* are the long-excurrent costa, the width and depth of the costa as seen in transverse-section, the size of the papilla found on the abaxial surface of the lamina and costa, and its specialized habitat. The costa is always long-excurrent, sometimes being 1/3 of the leaf length while that of *D. fuscescens* is usually percurrent or only slightly excurrent. The costa of *D. fuscescens* often appears more excurrent than it actually is since the leaf is narrowly-lanceolate. Close examination typically shows one or two rows of laminal cells extending along the costa to the leaf tip. These laminal cells do not extend as far in *D. sulcatum* and the area is occupied by costal cells. The difference between these two species is easily quantified by examining the costa in median transverse-section (Figs. 27-13, 29-13). *Dicranum sulcatum* has a costa width ranging from 85-115 µm at this point in the leaf, while *D. fuscescens* has a costa width ranging from 75 - 90 µm at the same position. In addition, the depth of the costa at the same point is 40 - 60 µm in *D. sulcatum* and 30 - 50 µm in *D. fuscescens*. The difference in costa volume is a result of more stereid cells in *D. sulcatum* where each stereid bundle consists of 3 to 5 rows of cells (Fig: 29-13), while the stereid bundles of *D. fuscescens* (Fig. 27-13) seldom contain more than two rows of stereid cells. The larger number of stereid cells in the costa of *D. sulcatum* usually give the specimens a more pronounced keel to the leaves than that found in *D. fuscescens*.

Macroscopically, many specimens of *D. sulcatum* appear a darker, duller colour than *D. fuscescens*, and this is partially due to the greater degree of papillosity. Papillose surfaces do not reflect light as well as smooth surfaces. The papillae are most easily seem in transverse-section and range in size from 3 - 8 µm in height on *D. sulcatum* (Fig. 29-13) as compared to 0 - 3 µm on *D. fuscescens*. Finally, thehabitat of *D. sulcatum* is unique within the genus. It is

FIGURE 29. *Dicranum sulcatum* Kindb.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9,10	Capsules (10x)
11	Peristome tooth (180x)
12	Upper transverse-section (280x)
13	Median transverse-section (280x)

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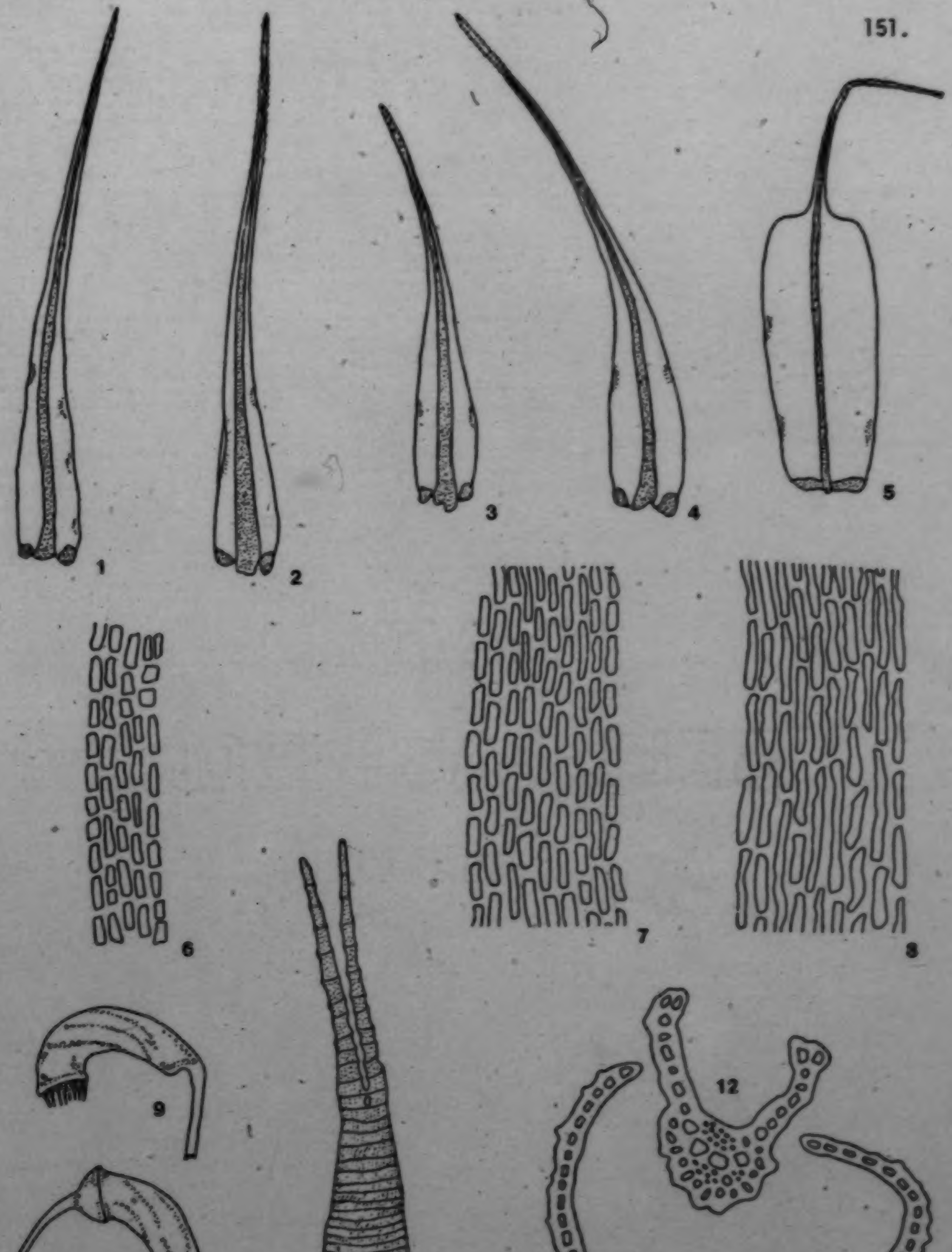
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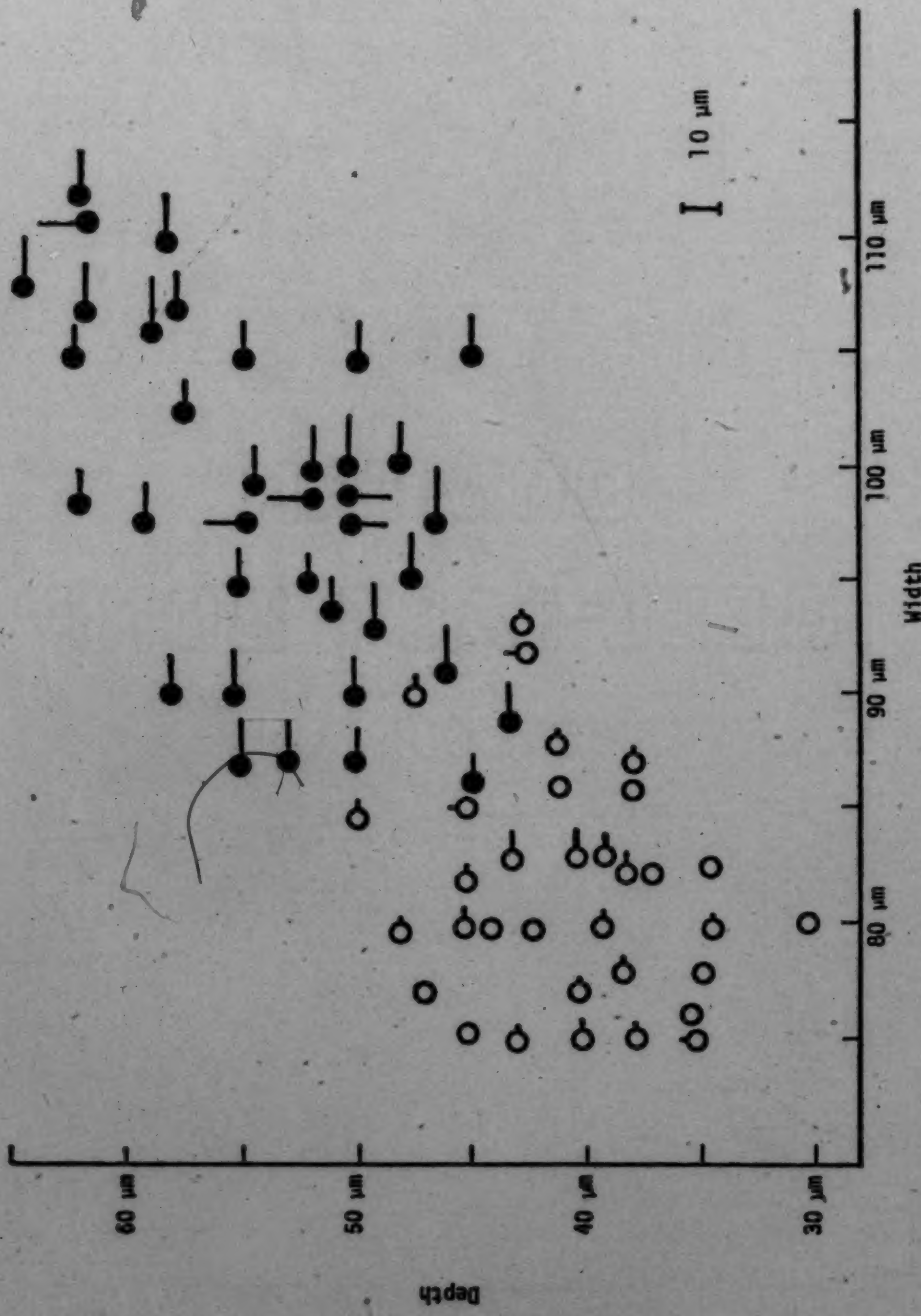
FIGURE 30. A comparison of costa width, depth, and papillae size in *Dicranum fuscescens* Turn. and *Dicranum sulcatum* Kindb. The data were recorded from median transverse-sections. Solid circles (●) represent specimens with a long, excurrent costa and growing on living trees or logs. Open circles (○) represent specimens with a percurrent costa and growing on logs and humus. Tails on the dots represent papillae size. Each dot represents the mean of five measurements taken from a single population.



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the only species that generally grows on living trees although there is one species in the closely related genus *Orthodicranum* (*O. viride*) which grows on living angiospermous trees in eastern North America. *Dicranum sulcatum* grows on living coniferous trees and this may be useful in field identifications.

According to the original description (Macoun and Kindberg, 1892), *D. crispulum* differs from *D. sulcatum* in having shorter stems, a slightly less excurrent costa and smaller alar cells. After examining the type, I feel that the species falls well within the concept of *D. sulcatum* and therefore, I have included it as a synonym of *D. sulcatum*.

9. *Dicranum pallidisetum* (Bailey) Ireland, Bryologist 68: 446. 1965.

Dicranum fuscescens forma *pallidiseta* Bailey *in* Holz., Musci Acroc. Bor. Amer. et Eur. 653. 1929.

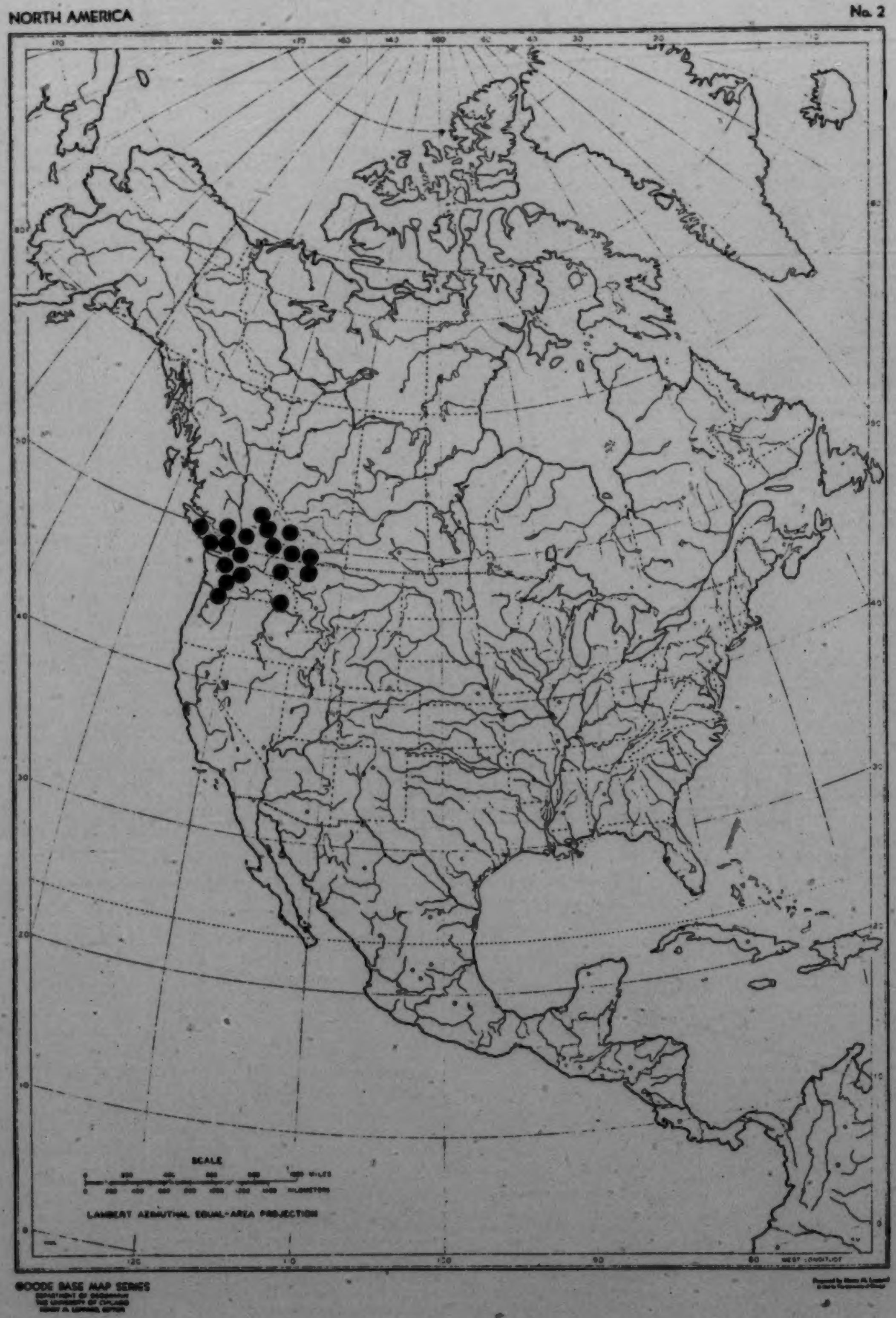
Type: "Mt. Margaret, Wolf Creek, Washington."
(Lectotype-MIN!; Isotype-UC!)

Plants in loose to dense tufts up to 5 cm tall, dark-green, glossy, growing on humus or soil. Stems sparsely tomentose, tomentum white to brown. Leaves when dry falcate-secund and slightly twisted, when moist falcate-secund to straight, not undulate, (3.0) 4.5-8.0 mm long, lanceolate, tapering to a sharply acute tip, tubulose, not keeled, smooth or rarely papillose on upper abaxial laminal surface; margins serrate or entire, unistratose or sometimes bistratose in spots in upper 1/3; costa wide, 175-230 (250) µm just above alar region, percurrent, toothed on upper abaxial surface, costa in transverse-section showing 7 to 9 guide cells and no stereid bands, cells above and below guide cells large and thin-walled, stereid bands sometimes present in the lower 1/4 - 1/5 of leaf; alar cells brown, bistratose, thin-walled, often reaching costa; basal cells above alar region rectangular, thin-walled, smooth (30) 55-110 μm long, median cells short-rectangular, in uniform rows, extending 2/3 the way to the base, thin-walled (15) 20-40 μm, not pitted, upper cells similar to median or slightly smaller (10) 15-40 μm, thin-walled. Perichaetial leaves abruptly tapering to a short subulate tip.

Dioicous, male plants as large as female plants. Monosetous, setae yellow, 1.0-3.0 cm long. Capsules yellow to light-brown, 2.5 -3.5 mm long, curved, strongly ribbed, ribs often dark-brown, neck short, strumose; exothecial cells rectangular, thick-walled; stomates in one row at base of capsule, 24-34 μm long; operculum rostrate, 1.0-1.5 mm long; annulus of 1 to 3 rows of enlarged, hyaline, thick-walled cells, peristome teeth orange to red, vertically striate, ±0.5 mm long, 75-90 (110) μm wide at base, divided about half way down into 2 segments. Spores green to brown, lightly papillose, (12) 15-20 μm. Chromasome number, n=12.

Habitat and Distribution (Fig. 31): This species is endemic to northwestern North America and has been collected in southern British Columbia, southwestern Alberta (Waterton National Park), Washington, northern Oregon, northern Idaho, and northwestern Montana. It is usually found growing on soil or humus at higher elevations (>1000

FIGURE 31. The known distribution of *Dicranum pallidisetum* (Bailey) Ireland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meters) as shown by many of the collection localities such as Whistler Mtn. and Rogers Pass in British Columbia, Stevens Pass and Stamped Pass in Washington, and the slopes of Mt. Hood in Oregon.

Selected Specimens Examined: EXSICCATI. Holzinger, Musci, Acroc. Bor. Amer. et Eur. 534 as *D. fuscescens* forma *pallidiseta* (MIN, UC).

CANADA. Alberta: Waterton Lakes National Park, Cameron Lake Region, Ireland 9531 (CANM). British Columbia: Whistler Mtn., Schofield and Worley 35532 (UBC). Grouse Mtn., Schofield 43101 (UBC). Mt. Seymour, Mueller 6781 (UC). Glacier, Nakimu Caves, MacFadden, July 25, 1941 (DUKE). Roger's Pass, Krajina 65062171 (CAS).

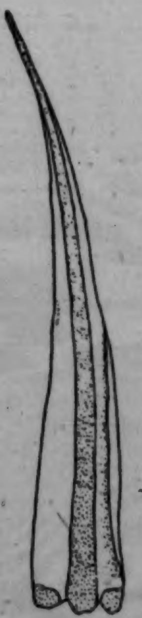
U.S.A. Idaho: Bonner Co., Daubenmire 4317 (F). Montana: Glacier National Park, Fish Lake, Yuncker and Yuncker 7-086 (DUKE). Oregon: Clackamas Co., Mt. Hood Road to timberline lodge, Hermann July 11, 1963 (WTU). Hood River Co., Mt. Hood, Still Creek Forest Camp, Svihla 4754 (WTU). Washington: Stevens Pass, Leiberg 390 (US). Kittitas Co., Stampede Pass, Ireland 9472 (LAF). Lewis Co., Mt. Rainier, Ireland 8231 (WTU). Kings Co., Silver Peak Trail, Bailey 534 (UC). Snoqualmie Pass, Frye 3199 (CAS).

Dicranum pallidisetum was first described as a form of *D. fuscescens* in Holzinger's Acrocarpi Boreali-Americani et Europeae exsiccati set from a specimen collected by J.W. Bailey. A short but valid description was included on the exsiccati label and stated "capsule and seta light yellow". Ireland (1965) elevated the taxon to the specific level based on additional morphological and ecological information. He discussed the brief description and the additional note on the label which states "See Bryologist p. I 1929". Since there is no reference to the material in the 1929 Bryologist or any other year, and Holzinger died in May 1929, Ireland concluded that the article referred to was never published. As a result, it is impossible to ascertain who was the first to recognize the taxon as distinct and who provided the description on the label.

Ireland (1965) discovered that the internal costal morphology was quite different from that of typical *D. fuscescens* in that *D. fuscescens* forma *pallidiseta* lacks stereid bands in the upper half of the leaf (Figs. 32-12, 32-13). He used this data to support specific status of the taxon. I agree with Ireland that *D. pallidesetum* is a distinct species. It is the only member of the genus that lacks stereids in the upper half of the leaf. In addition, the seta and capsules are yellow (as stated in the original description), which is a character state not found in any closely related species. The only other *Dicranum* species to have yellow setae and capsules is *D. condensatum*, an unrelated species endemic to eastern North America. Also, the leaves of *D. pallidisetum* are tubulose (Fig. 32-12) like *D. muehlenbeckii*, not keeled like *D. fuscescens* (Fig. 27-13). The capsules have a short neck and struma similar to that of *D. fuscescens*.

FIGURE 32. *Dicranum pallidisetum* (Bailey) Ire.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)
13	Upper transverse-section (280x)
14	Basal transverse-section (280x)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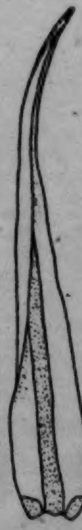
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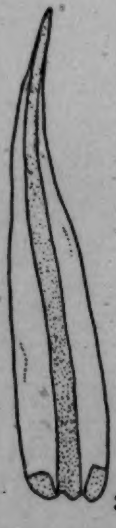
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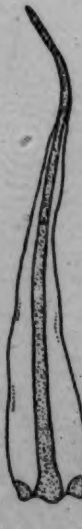
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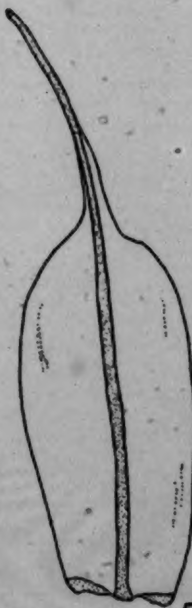
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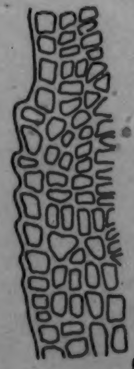
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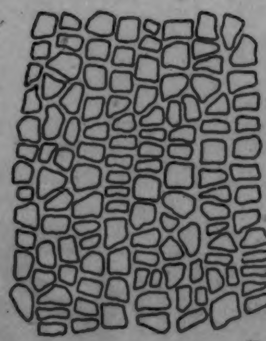
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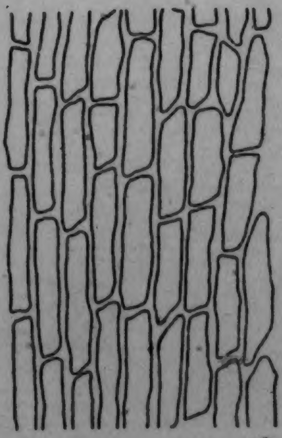
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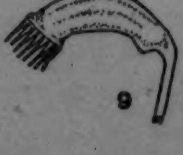
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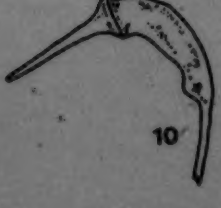
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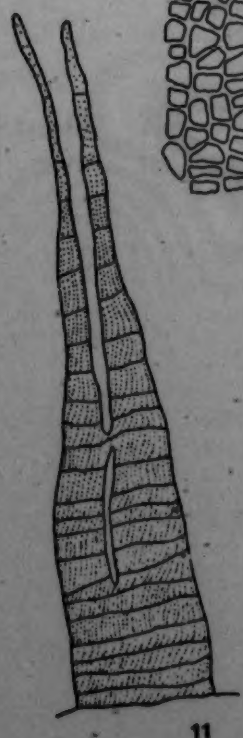
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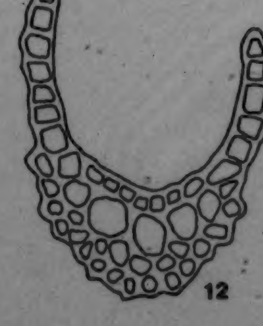
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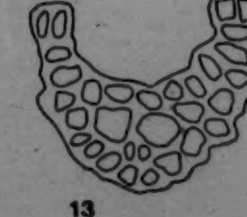
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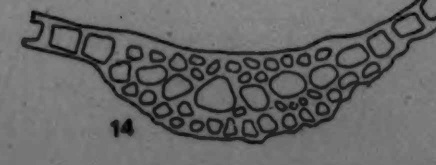
14

Section: *Muehlenbeckia* Peterson *Sect. nov.**

Lectotype: *Dicranum muehlenbeckii* B.S.G.

Costa in sectione transversali cum stereidas. Stereidae lumina grande. Capsulae non strumosae; collorum longorum.

Plants up to 8 cm tall. Leaves not undulate, falcate-secund to erect, occasionally twisted, lanceolate, apex acute, percurrent to excurrent; upper lamina cells short-rectangular to quadrate, corners often rounded, walls smooth or pitted; median transverse-section of costa showing one row of guide cells and two stereid bands, lumens of stereids large (about equal to the wall thickness). Capsules curved, ribbed, neck long; annulus present.

10. *Dicranum muehlenbeckii* B.S.G., Bryol. Eur. Fasc. 37-40. 1: 148. 1847.

Type: "*Tusis Rhaetiae et Tiefenkastel ... Muehlenbeck ... 1844, detexit.*" (Lectotype-BM! *ex* herb Schimper).

Dicranum rauii Austin, Bot. Gaz. 1: 28. 1876.

Type: "Colorado, 1875, Brandegee (Rau)." (Lectotype-NY!)

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*To be validly published at a later date.

Plants in loose mats or small tufts, up to 6 cm tall, light-to dark-green, 3 — 7 cm tall, growing on soil or humus. Stems lightly tomentose, tomentum light-brown. Leaves when dry falcate-secund to erect, similar when moist, somewhat concave, not undulate, 4-6 (6.5) mm long, lanceolate to ovate-lanceolate, tapering to an acute tip, tubulose, not keeled, smooth on both surfaces; margins entire to serrulate in upper 1/3, unistratose; costa narrow, 100-120 μm wide just above alar region, percurrent or slightly excurrent, papillose on upper abaxial surface; costa in median transverse-section showing 6 to 8 guide cells and 2 moderately developed stereid bands, both bands extending well into the apex, both adaxial and abaxial layer of external cells differentiated from stereid cells by larger lumens; alar cells brown, bistratose, thin-walled, not reaching costa; basal cells above alar region rectangular, (40) 60-100 μm long, thin-walled, pitted; median cells rectangular, or irregularly angled, 24-50 (50) μm long, pitted; upper cells short, rectangular, sometimes slightly irregular, smooth or pitted, 10-20 μm long. Perichaetial leaves shorter than stem leaves, the innermost abruptly narrowed to a subulate tip.

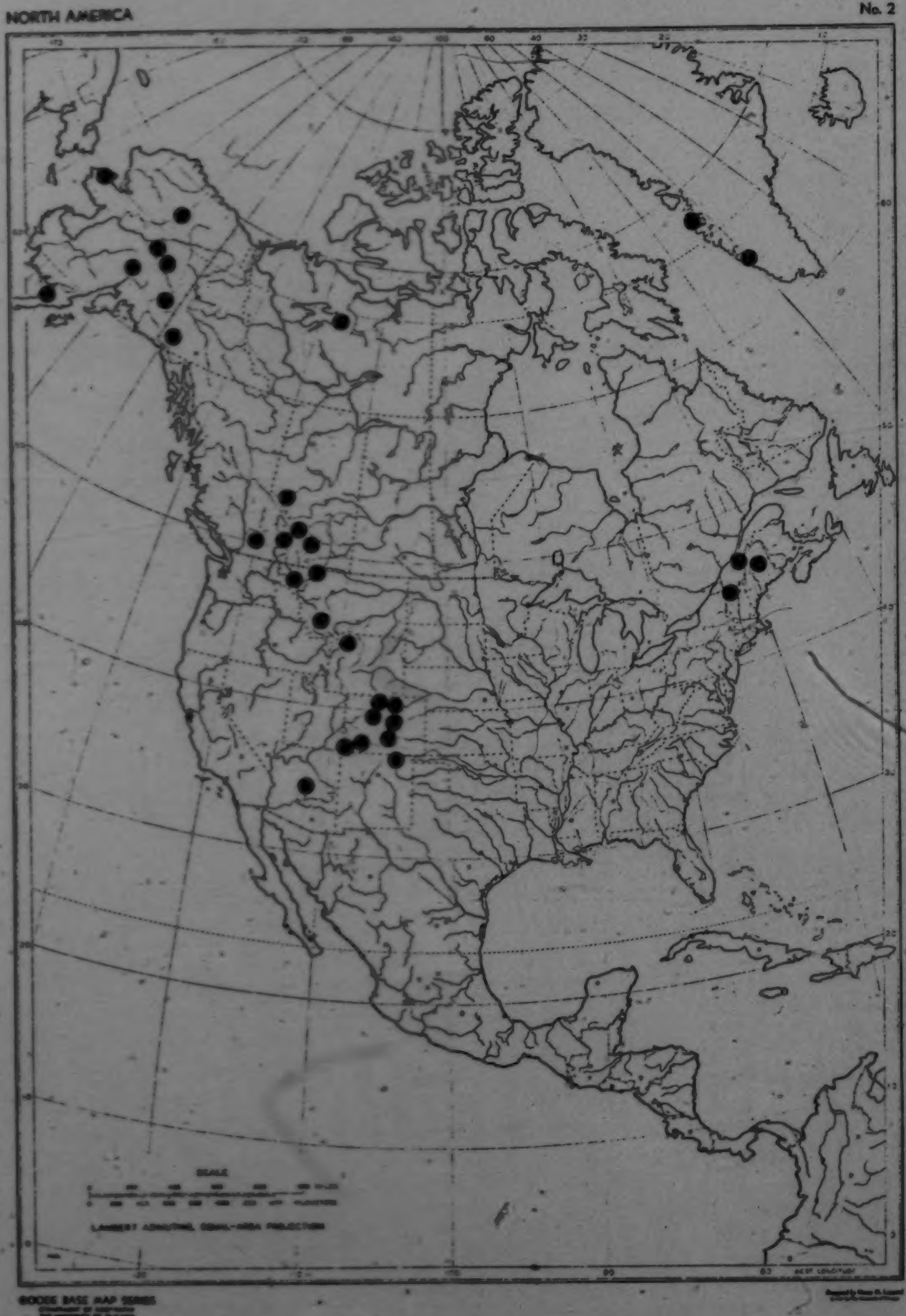
Dioicous, male plants as large as female plants. Monosetous, setae light-to dark-brown, 1.8-2.5 cm long. Capsules brown to yellow, 2.5-3.2 mm long, curved, ribbed, not strumose, neck long; exothecial cells long-rectangular, about 90 μm, thin-walled, slightly pitted; stomates few, in one row at base of capsule, 36-38 μm long; opercula rostrate, 1.5-2.0 mm long; annulus of 2 to 3 rows of large, thick-walled hyaline cells; peristome teeth orange to red, about 0.5 mm long, 85-95 µm wide at base, vertically striate, divided 1/2 way down into 2 segments. Spores lightly papillose, 15-20 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 33): This species is found in moist, sheltered habitats at moderatley high elevations, but usually below timberline. It has been collected in the Rocky Mountains from northern New Mexico north to Banff, Alberta as well as in the mountains of Alaska. It probably occurs in the mountains between Alaska and Alberta although I have not seen specimens from this area. In addition, it has been found near Great Bear Lake in the Northwest Territories, Greenland, and the mountains of Maine, Vermont, and the Gaspé region of Quebec. It is to be expected in the mountains of Labrador. It is also reported from the mountains of Europe, Scandinavia, the Caucasus of eastern Asia, and the Siberian Arctic.

Selected Specimens Examined: EXSICCATI. Holzinger, Musci Acroc. Bor. Amer. et Eur. 560 (US, UC). Sull. and Lesq., Musci Bor. Amer. ed. 2 81 (F).

CANADA. Alberta: Bow River Watershed, Wilkinson Creek beside Kananskis-Coleman road, Bird and Glenn 14202 (CANM). Pipestone Pass, July 6, 1904 (Collector Unknown) (DUKE). British Columbia: Salmon River, Brinkman 388 (DUKE). Rogers Pass, Brinkman, July 2, 1918 (CAN). Beside Banff National Park, 51°02'N, 115°47'W, Scotter 11487 (CANM). Quebec: Mt.

FIGURE 33. The North American distribution of *Dicranum muehlenbeckii* B.S.G.


NORTH AMERICA
No. 2
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES

Anselema, Dunham A-118 (DUKE). Northwest Territories: Great Bear Lake, Port Radium, 66°05'N, 118°02'W, Steere 10011 (CANM).

U.S.A. Alaska: Mt. McKinley National Park, Hermann 21331 (US). Fairbanks, Hermann 21034 (MICH). Tolovana River, West Fork, Shacklette 5732 (MICH). Wiseman, Crum 2153 (MICH). Maclaren Glacier, Shaklette 5550 (MICH). Arizona: Cogonito Co., Humphrie's Peak, Haring 10456 (ARIZ). Colorado: Gilpin Co., Corona, Grout Jan. 1937 (DUKE). Larimer Co., La Poudre River, Hermann 16997 (US). Hinsdale Col., White Cross Mtn., Livingston 255 (DUKE). Pike's Peak, Holzinger 560 (US) Boulder Co., Silver Lake, Weber and LaFarge B43726 (LAF). LaPlata Co., Animas River, Michener 210 (COLO). Clear Creek Co., Summit Lake, Weber *et al.* B11037 (COLO). Maine: Mt. Katahdin, Lorenz Aug. 29, 1916 (DUKE). Montana: Glacier Co., Logan's Pass, Hidden Lake overlook, Hermann 18096½ (DUKE). Columbia Falls, Williams Sept. 30, 1895 (F). Madison Co., 19.2 km E of Beaverhead National Forest, Hermann 17935 (WTU). New Mexico: Wheeler Peak, Hermann 23969 (DUKE). Vermont: Burlington, Rock Point, Grout June 14, 1897 (TENN). Wyoming: Yellowstone National Park, Madison Junction, Conard Aug. 18, 1953 (CANM).

Dicranum muehlenbeckii is closely related to two species, *D. brevifolium*, and *D. spadiceum*. It is separable from the former by its tubulose leaves, while those of *D. brevifolum* are keeled, The other closely related species, *D. spadiceum*, has tubulose leaves similar to those of *D. muehlenbeckii* and the two may be difficult to separate, although they do differ in a number of ways. These differences are listed in Table 7 and several graphically displayed in Fig. 35. The most significant character which separates these two species is the width of the costa when measured just above the alar region, with that of *D. muehlenbeckii* ranging from 95-120 µm wide while that of *D. spadiceum* ranges from 65-85 µm wide. The other gametophytic characters listed in Table 7 overlap slightly between the two species; however, when they are used in conjunction with the costa width (Fig. 35) the differences can be seen. The costa as seen in median transverse-section is different between the two, since that of *D. muehlenbeckii* always has the adaxial layer of external cells differentiated from the stereid cells by larger lumens (Fig. 34-12) while that of *D. spadiceum* only rarely has a few cells in this layer differentiated from the stereids (Fig. 37-12). The median and upper laminal cells of *D. spadiceum* are also somewhat longer than the cells of similar areas in *D. muehlenbeckii*. There also seems to be a difference in spore size although only a limited number of specimens that were examined had sporophytes present. Those of *D. muehlenbeckii* had spore sizes ranging from 15 — 20 µm while those of *D. spadiceum* has spore sizes ranging from 20 - 24 µm.

FIGURE 34. *Dicranum muehlenbeckii* B.S.G.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)

170.

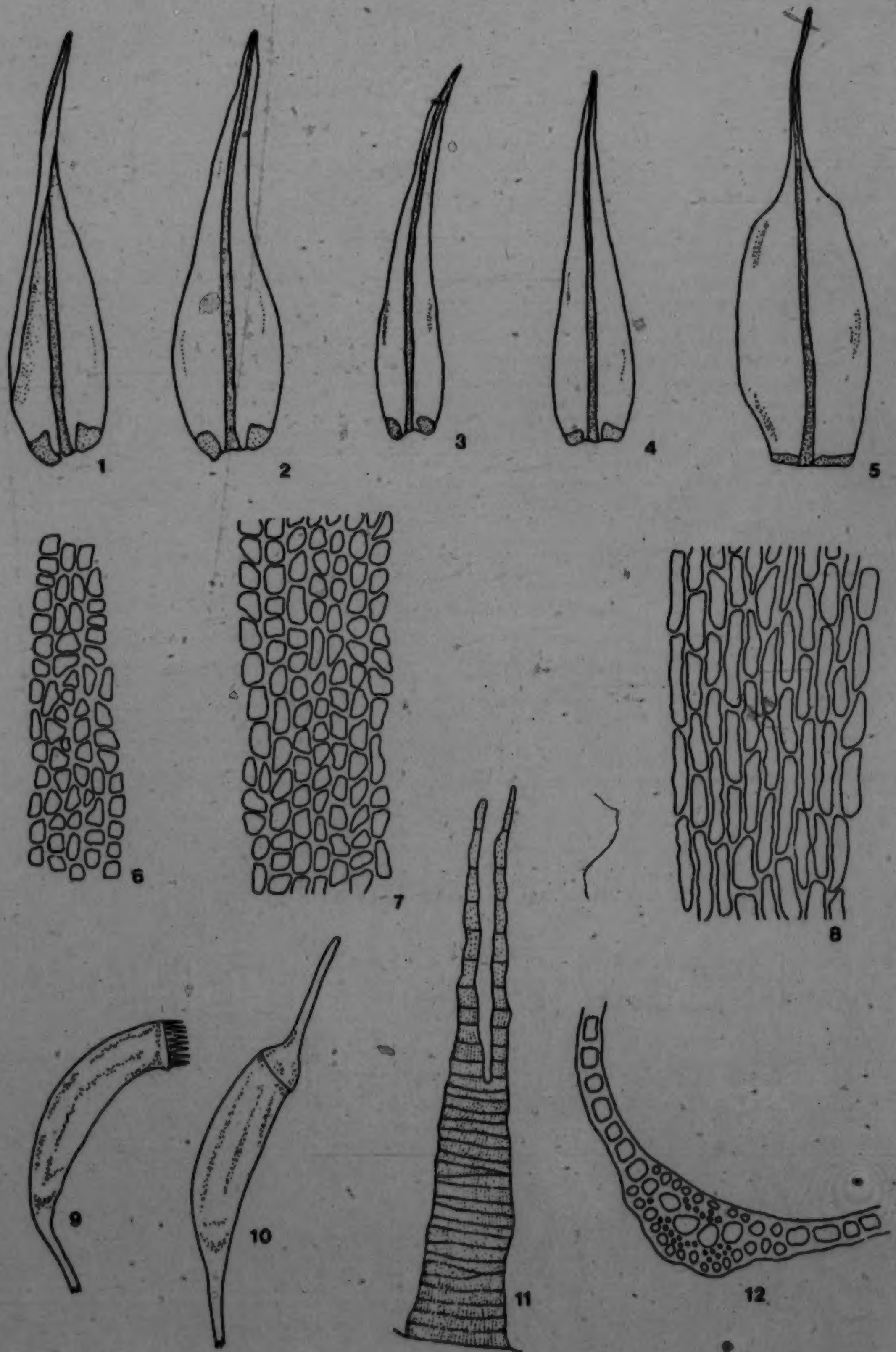

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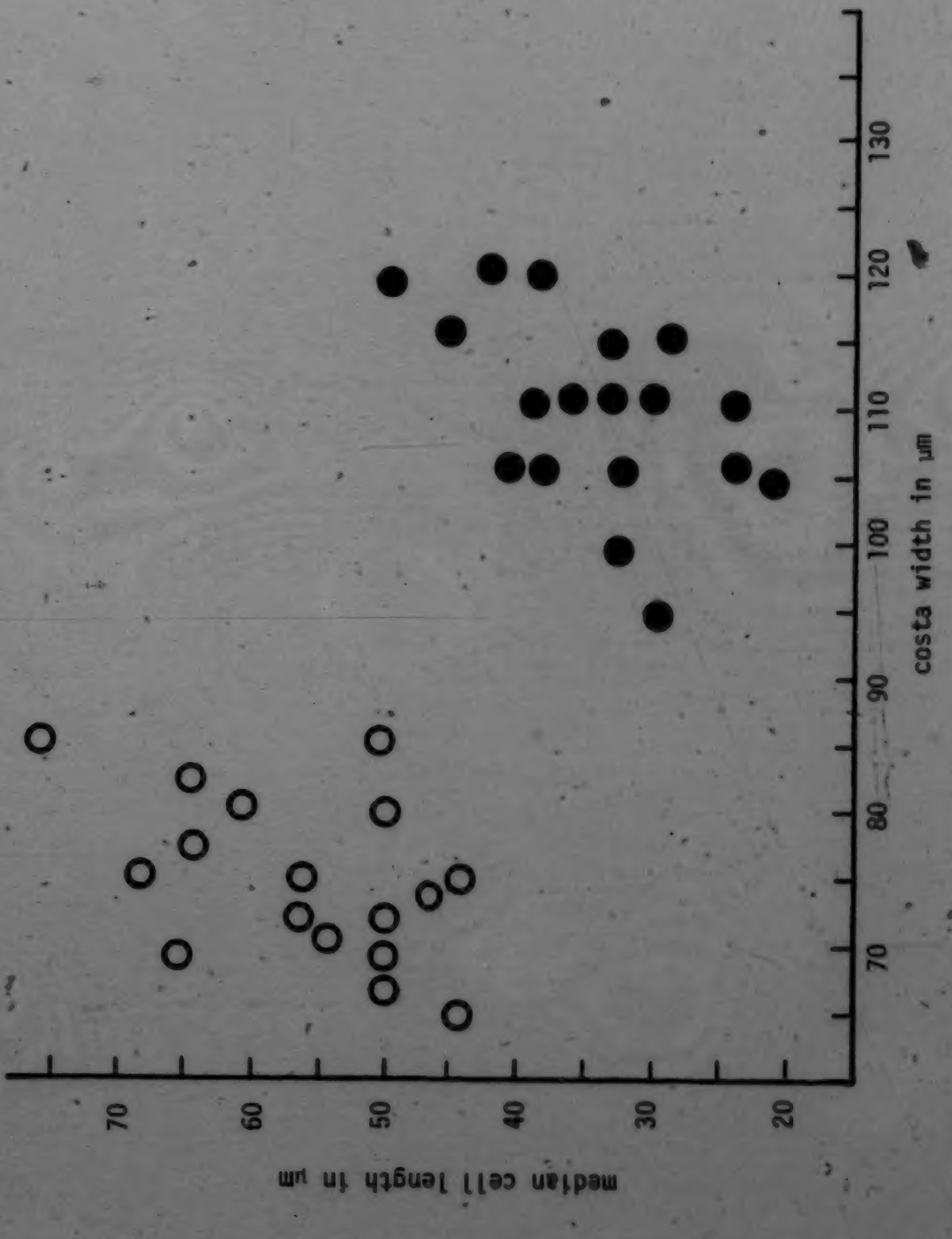
TABLE 7. Differences used in separating *Dicranum muehlenbeckii* from *D. spadiceum*.

	D. muehlenbeckii	*D. spadiceum*
Leaf length	4-6 mm	5-9.5 mm
Costa width	95-120 µm	65-85 µm
Median cell length	20-40 µm	40-70 µm
Upper cell length	10-20 µm	20-35 µm
Adaxial layer of costal cells	Always differentiated	Rarely differentiated
Spore size	20-24 µm	15-20 µm

FIGURE 35. A comparison of costa width and median cell length in *Dicranum spadiceum* Zett. (○) and *Dicranum muehlenbeckii* B.S.G. (●). Costa measurements were taken from just above the alar region. Each dot represents the mean of 5 measurements taken from a single population.


median cell length in µm
70
60
50
40
30
20
costa width in µm
70
80
90
100
110
120
130

11. *Dicranum spadiceum* Zett., K. Sevensk. Vet. Akad. Handl. 5(10): 20. 1865.

Type: "Port de Venasque, Crabioules." (Holotype-UPS!).

Dicranum neglectum Juratzka, Laubm. 47. 1882.

Syntypes: "Ob Oest.: Pyrgas b. Spital a Pyhrn", Juratzka (W!). "Steierm: Reiting b. Leoben 1900 m." Breidler (W!); "Ruprechtseck in der Kraggau 2580 m." Breidler (W!); "Leignitzhöle, Schiedeck u. Hochgolling b. Schladming 1900-2850 m.", Breidler (W!). "Salzb.: Gamskarkogel b. Gastein", Preuer (W!); "Radstädter Tauern 1517 m.", Zwanziger (W!). "Tirol: Hafelekar b. Innsbruck", Kerner (W!); "Schlern b. Bozen 1900 m.", Milde (W!); "Hochalpe 'Saent'", Venturi (W!); "Mte. Confinale, Sobretta, Piz Ombral:, Lorentz (W!).

Dicranum muehlenbeckii B.S.G. var. *neglectum* (Juratzka) Pfeffer, Bryogeogr. Stud. 23. 1869.

Dicranum algidum Kindb., Rev. Bryol. 23: 17. 1896.

Types: "On rocks in alpine region. Amer. Canada, Rocky Mountains 2700 m above the sea", Macoun (Syntype-S!). "Eur. Sweden (Lapland) and Norway (Lille Elvedal)", E. Nyman.

Dicranum algidum Kindb. ssp. *subspadiceum* Kindb., Eur. N. Am. Bryin. 2: 199. 1897.

Type: "Rocks in Alp. r. Amer. Can. Rocky Mts., 2500 m.", Macoun (Holotype-S!).

Dicranum bambergeri Schimp. *in* Par., Ind. Bryol. 344. 1896. *Hom. illeg. inc. species prior.*

Dicranum Dentzelii Kerner ms.

Plants in loose mats or tufts up to 8 cm tall, dark-green to almost black, 2-8 cm tall, growing on soil or humus. Stems lightly tomentose, tomentum light- to dark-brown. Leaves when dry slightly falcate-secund, base of leaf usually concave, when moist erect or only slightly falcate-secund, not undulate, 5-8 (9.5) mm long, broadly lanceolate to ovate-lanceolate, tapering to an acute tip, tubulose, not keeled, smooth on both surfaces; margins entire, unistratose; costa narrow, 65-85 μm wide just above alar region, percurrent or rarely slightly excurrent, papillose on upper abaxial surface; costa in median transverse-section showing 5 to 7 guide cells and 2 moderately developed stereid bands, both bands extending well into the apex, abaxial layer of external cells differentiated from stereids by larger lumens, adaxial layer rarely with a few differentiated cells; alar cells brownish, bistratose, thin-walled, not reaching costa; basal cells just above alar region elongate-rectangular, 50-75 (110) μm long, thin- or thick-walled, pitted; median cells rectangular or slightly irregular angled, 40-60 (85) μm long, thin-walled, pitted; upper cells short-rectangular or occasionally slightly elongate, pitted, 20-35 (45) μm long; perichaetial leaves shorter than stem leaves, the innermost abruptly narrowed to a subulate tip.

Dioicous, male plants as large as female plants. Monosetous, setae, brown, 1.5-2.5 cm long. Capsules light- to dark-brown, 2.0-3.5 mm long, curved, ribbed, not strumose, neck long; exothecial cells long rectangular, about 40-50 μm long, thin-walled, slightly pitted; stomates few in one row at base of capsule, 32-34 μm long; opercula rostrate, about 1.5 mm long; annulus of 1-3 rows of large, thick-walled, hyaline cells; peristome teeth red, about 0.5 mm long, 65-80 (95) µm wide at base, vertically striate, divided 1/2 way down into 2 segments. Spores 20-24 µm, finely papillose. Chromosome number, n=12.

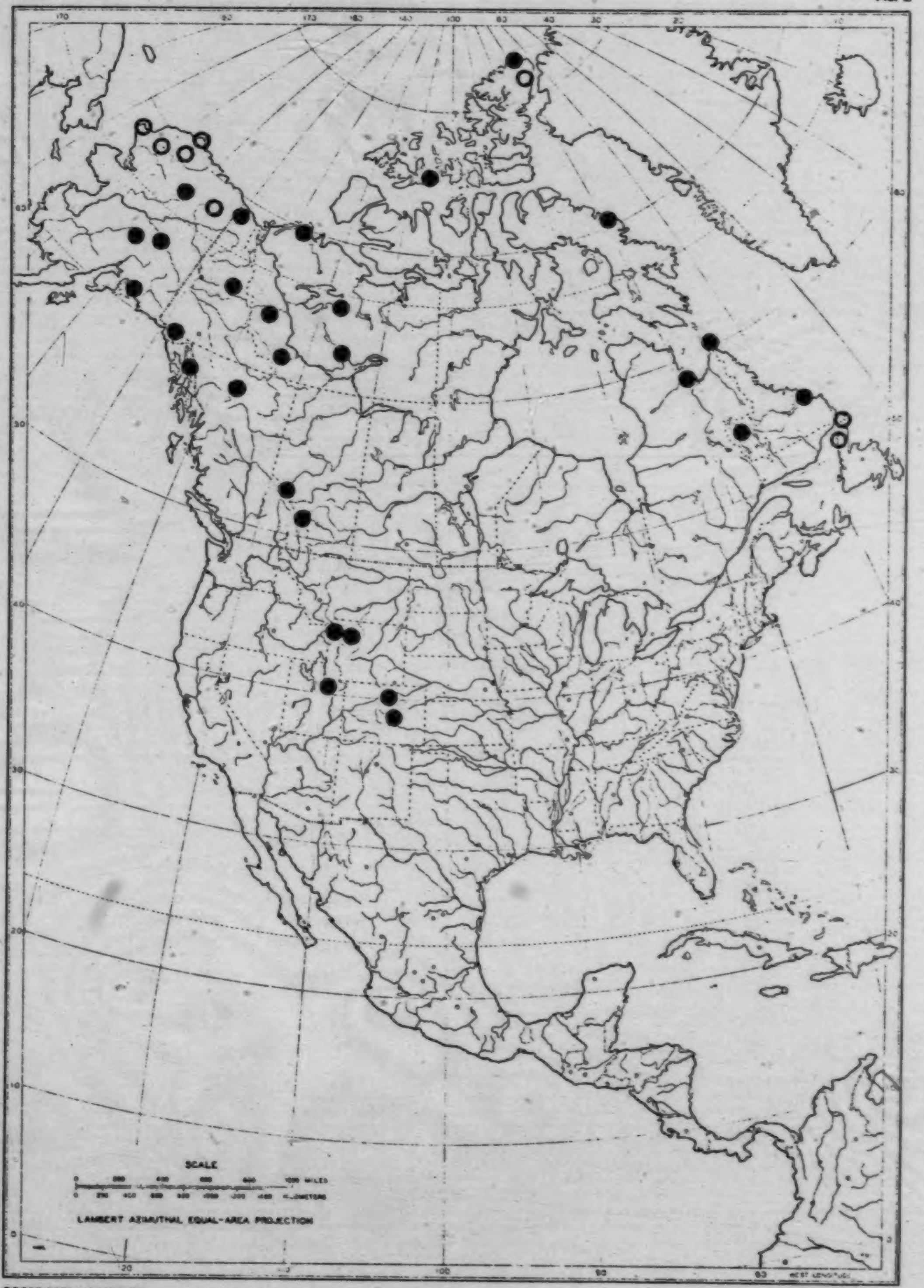
Habitat and Distribution (Fig. 36): *Dicranum spadiceum* is a species that grows primarily on soil or humus over or around rocks on the subalpine, alpine, and arctic regions. It has been collected in the Rocky Mountains of Colorado and northward into the Canadian Rocky Mountains of Alberta and northern British Columbia as well as the Wernecke Mountains of the Yukon Territory and the Brooks Range of northern Alaska. It also has been collected on Ellesmere Island and Baffin Island and probably occurs in a continuous pattern across the Arctic. Along the eastern coast of Canada, it has been collected in Labrador and northern Quebec. In Europe it is reported from Norway, Finland, Sweden, the Alps and the Pyrenees; in Asia it is found in Siberia and the Altai Mountains.

Selected Specimens Examined: CANADA. Alberta: Jasper National Park, Wilcox Pass, Lawton 1403 (WTU). British Columbia: Yoho Pass, Macoun 32a (US). Summit Lake, about 160 km W of Ft. Nelson, 124°43'W, 58°37'N, Peterson 3008 (ALTA). Muncho Lake Area, Alaska Hw. milepost 444.9 at Peterson Creek, 125°49'W, 58°52'N, Peterson 3111 (ALTA). Newfoundland: Labrador, Indian Harbor, Wicks 30 (US). Labrador, Mosquito Bay, 60°42'N, Low 9828 (CANM). Labrador, Scott Falls, 53°35'N, 64°20'W,

FIGURE 36. The North American distribution of *Dicranum spadiceum* Zett.

NORTH AMERICA

No. 2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0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
170
160
150
140
120
100
80
60
40
30
20
10
0
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40
30
20
10
90

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

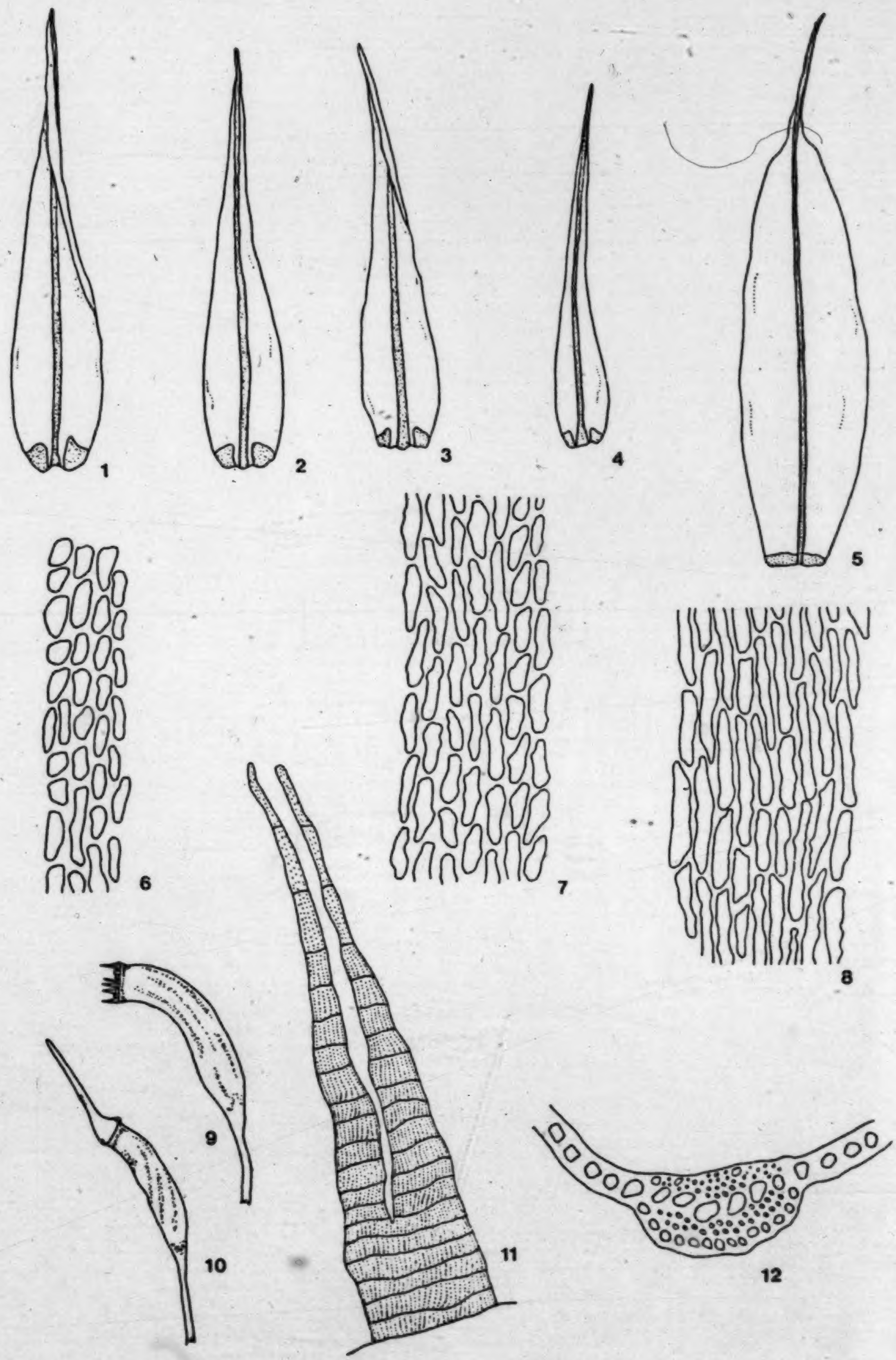
Prepared by Henry M. Leppard
[illegible]

Kallio June 27, 1963 (CANM). Quebec: Lac Gabriel, 58°06'N, 68°38'W, Ducruc 21-3 (CANM). Northwest Territories: Great Bear Lake, Port Radium, 66°05'N, 118°02'W, Steere 10011 (SMS). Anderson River, 69°18'N, 128°30'W, Scotter 5134 (CANM). Ward Hunt Island, 83°05'N, 74°00'W, Brassard 4328 (CANM). Keel River Region, 64°13'N, 127°24'W, Scotter 14254 (C). Yukon Territory: Kluane National Park, 60°38'N, 137°55'W, Scotter 18410 (C). Wernecke Mtns., 64°30'N, 135°06'W, Scotter 17986 (C). Firth River Basin, 68°40'N, 141°W, Sharp MC-58-157K (C).

U.S.A. Alaska: Fairbanks, Hermann 21085 (US). Juneau, Hermann 22028 (US). St. Matthew Island, Hanna July 8, 1916 (F). Mt. McKinley National Park, Viereck 3137 (MICH). Gubic, 69°28'N, 151°30'W, Steere 16234 (DUKE). Colorado: Boulder Co., Diamond Lake, Hermann 25915 (DUKE). Gilpin Co., Tolland, Grout July, 1914 (DUKE). Larimer Co., Redfearn 11413 (SMS). Montana: Flathead Co., Lake McDonald, 48 km E of Kalispell, Holzinger and Blake July 25, 1898 (MIN). Utah: Duschesne Co., Ottoson, Flowers 9638 (COLO). Wyoming: Yellowstone National Park, Host Creek Falls, Nelson and Nelson 5936 (US). Park Co., Long Lake, Weber B44283 (MICH).

FIGURE 37. *Dicranum spadiceum* Zett.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)



12. *Dicranum brevifolium* (Lindb.) Lindb., Musc. Scand. 24. 1879.

Dicranum muehlenbeckii var. *brevifolium* Lindb., Bot. Not. 80. 1865.

Type: "Norway, col. Blytt". (Isotype-H!).

Dicranum congestum var. *cirratum* Schimp., Coroll. 16. 1856.

Types: "In summis Alpibuse gr. in Helvel. Alp. Gemmi prope Schwarenbach (Sch.) in summo Stockhorn (Bamberger), in Sueciae provinc. Jemtlandia (R. Hartman). (Isosyntype-BM!)

Dicranum muehlenbeckii var. *cirratum* (Schimp.) Lindb. *in* Norrl., Medd. Soc. F. Fenn. 2: 20. 1878.

Dicranum cirratum (Schimp.) Lindb., Medd. Soc. F. Fl. Fenn. 6: 206. 1881. *Hom. illeg.*

Dicranum brevifolium is a species that might easily be taken for either *D. fuscescens* or *D. muehlenbeckii* since it has short upper cells similar to the former and capsules with long necks as in the latter. Nevertheless, both of its varities are easily distinguished from these species by several characters which are best summarized in the following key.

1. Leaves tubulose (costa not a prominent ridge on abaxial leaf surfaces) .... *Dicranum muehlenbeckii*

1. Leaves keeled (costa prominent as a ridge on abaxial leaf surface) 2

2. Median costal transverse-section showing strongly developed, small lumended stereids (Fig. 13-1), laminal cells with flat and smooth walls .... *D. fuscescens*

2. Median costal transverse-section showing moderately developed, large lumened stereids (Fig. 13-2), laminal cells with bulging walls that form papillae or ridges 3

3. Upper lamina unistratose; margins occasionally bistratose locally ... *D. brevifolium* var. *brevifolium*

3. Upper lamina bistratose or at least with numerous bistratose spots; margins bistratose or occasionally tristratose locally .... *D. brevifolium* var. *bistratosum*

The development of the stereids in *D. brevifolium* (Fig. 13-2) is similar to that of *D. muehlenbeckii* and *D. spadiceum* in that the lumens are not as small as the lumens of other members of the genus (Fig. 13-1). In addition, a transverse-section of *D. brevifolium* shows that the papillae are formed by protruding middle cell walls (Fig. 39-13) instead of thickening over the cell lumens. The papillae often coalesce into ridges that obscure cell arrangement (when examined in surface view) and at times may give a bistratose appearance to the leaves. This makes it necessary to examine specimens by transverse-section to determine if the apex area is actually bistratose, in which case, it would be *D. brevifolium* var. *bistratosum*.

Nomenclature: The basionym *D. congestum* var. *cirratum* Schimper predates that of *D. muehlenbeckii* var. *brevifolium* Lindb.; however, the name *D. cirratum* may not be used for this taxon at the specific level since it was previously used for another species (*D. cirratum* (Hedw.) Timm *ex* Gaertn., 1802) which is now recognized as *Dicranoweisia cirrata* (Hedw.) Lindb. *ex* Milde.

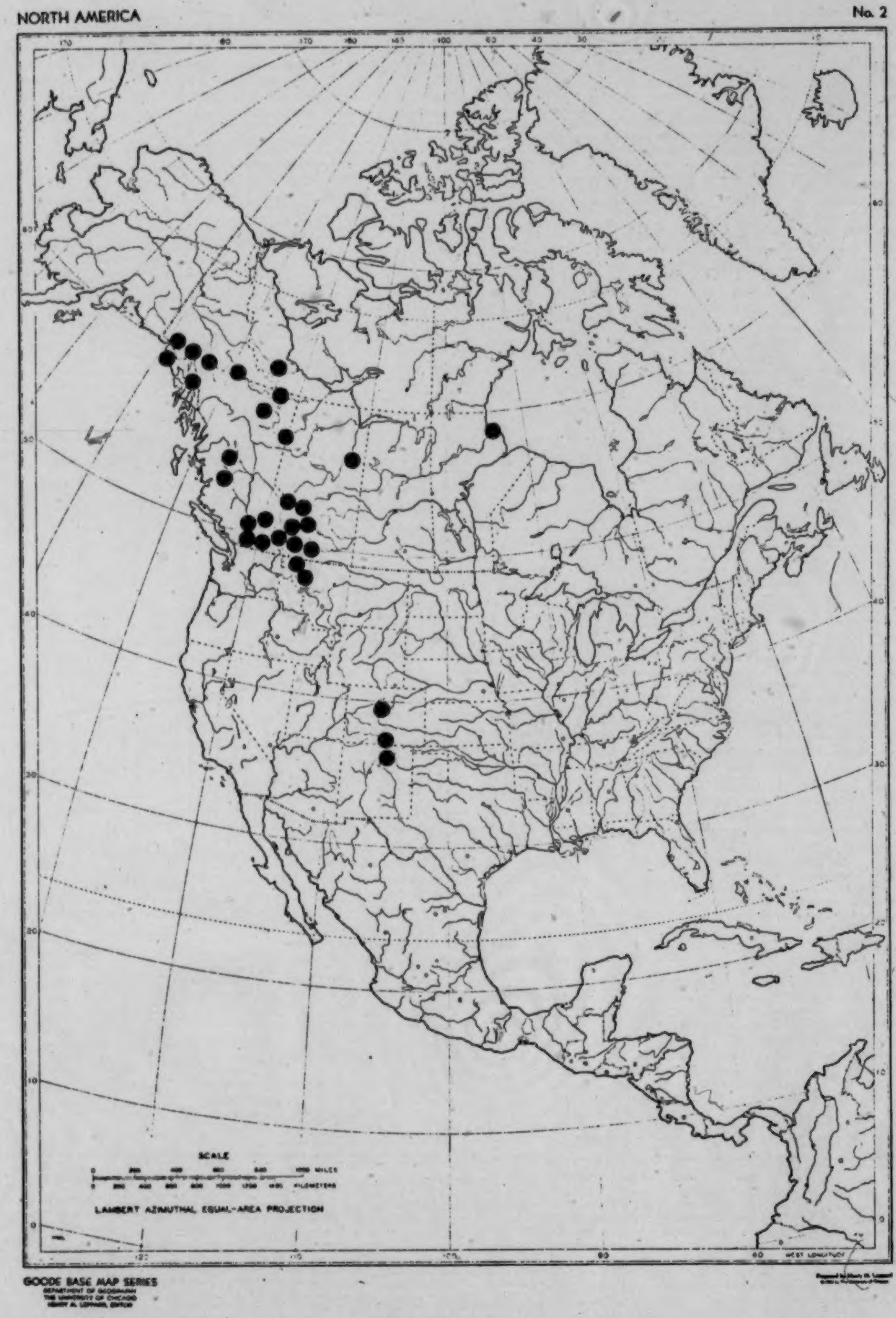
12a. *Dicranum brevifolium* (Lindb.) Lindb. var. *brevifolium*.

Plants in dense mats or tufts, up to 4 cm tall, light-green to dark-green, growing on soil or humus. Stems densely tomentose, tomentum brown to orange, often matted. Leaves when dry crisped to fulcate-secund, when moist usually straight and slightly spreading, sometimes falcate-secund, not undulate, 4.0-6.5 (8.5) mm long. lanceolate to long-lanceolate, tapering to an acute tip, keeled in upper half, middle cell walls often bulging to form papillae or ridges; margins entire to serrulate, unistratose or bistratose; costa wide, 150-165 μm wide just above alar region, percurrent or slightly excurrent, slightly toothed on abaxial surface, in median transverse-section showing 6 to 8 guide cells and 2 moderately developed stereid bands, both bands extending well into the apex, each band consisting of 2 or 3 cell layers, the abaxial layer of external cells slightly differentiated from stereids by large lumens, the adaxial layer not differentiated; alar cells brown, bistratose, thin-walled, sometimes extending to the costa; basal cells above alar region rectangular to short-rectangular, smooth or slightly pitted, thin- or thick-walled, 50-70 μm long; median cells short-rectangular, corners often rounded, in fairly uniform rows, extending about 2/3 to 4/5 the distance to the leaf base, thin- to thick-walled, (5) 10-20 µm long, cell walls usually bulging; upper cells similar to median, unistratose. Perichaetial leaves shorter than stem leaves, innermost ones abruptly narrowed to a subulate tip.

Dioicous, male plants similar to female plants. Monosetous, setae brown, 1.5-2.5 cm long. Capsules brown to dark-brown, 2.0-2.5 mm long, curved, ribbed, not strumose, neck long; exothecial cells rectangular, thick-walled, walls slightly pitted, 30-70 µm long; stomates few, in one loose row at base of capsule, 31-35 µm long; opercula rostrate, curved, 1.0-1.5 mm long; annulus of one or two rows of enlarged, thick-walled, hyaline cells; peristome teeth dark-red, vertically striate, about 0.5 mm long, 65-80 (95) µm wide at base, divided half way down into 2 segments. Spores papillose, 14-20 (22) µm. Chromosome number n=12.

Habitat and Distribution (Fig. 38): *Dicranum brevifolium* var. *brevifolium* is typically found in protected, rocky, habitats in montane or subalpine regions. It has been most frequently collected in British Columbia and Alberta at elevations above 1500 meters in sparce *Picea glauca* forests. More specifically, the habitat is usually fairly open, not densely covered by a forest canopy, and relatively exposed to sunlight. Also, the sites are usually such well drained areas as ridges and slopes. In North America, the type variety also occurs as far north as the southwest corner of the Yukon

FIGURE 38. The North American distribution of *Dicranum brevifolium* Lindb. var. *brevifolium*


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
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Territory and the Nahanni area in southwestern N.W.T., and as far south as northern New Mexico. Somewhat disjunct specimens have been collected in boreal forest habitats at Ft. McMurray, Alberta and Ft. Churchill, Manitoba, but it does not seem to be common in these areas. It is also reported from the European Alps, Finland, Norway, and western and eastern Asia (including Siberia).

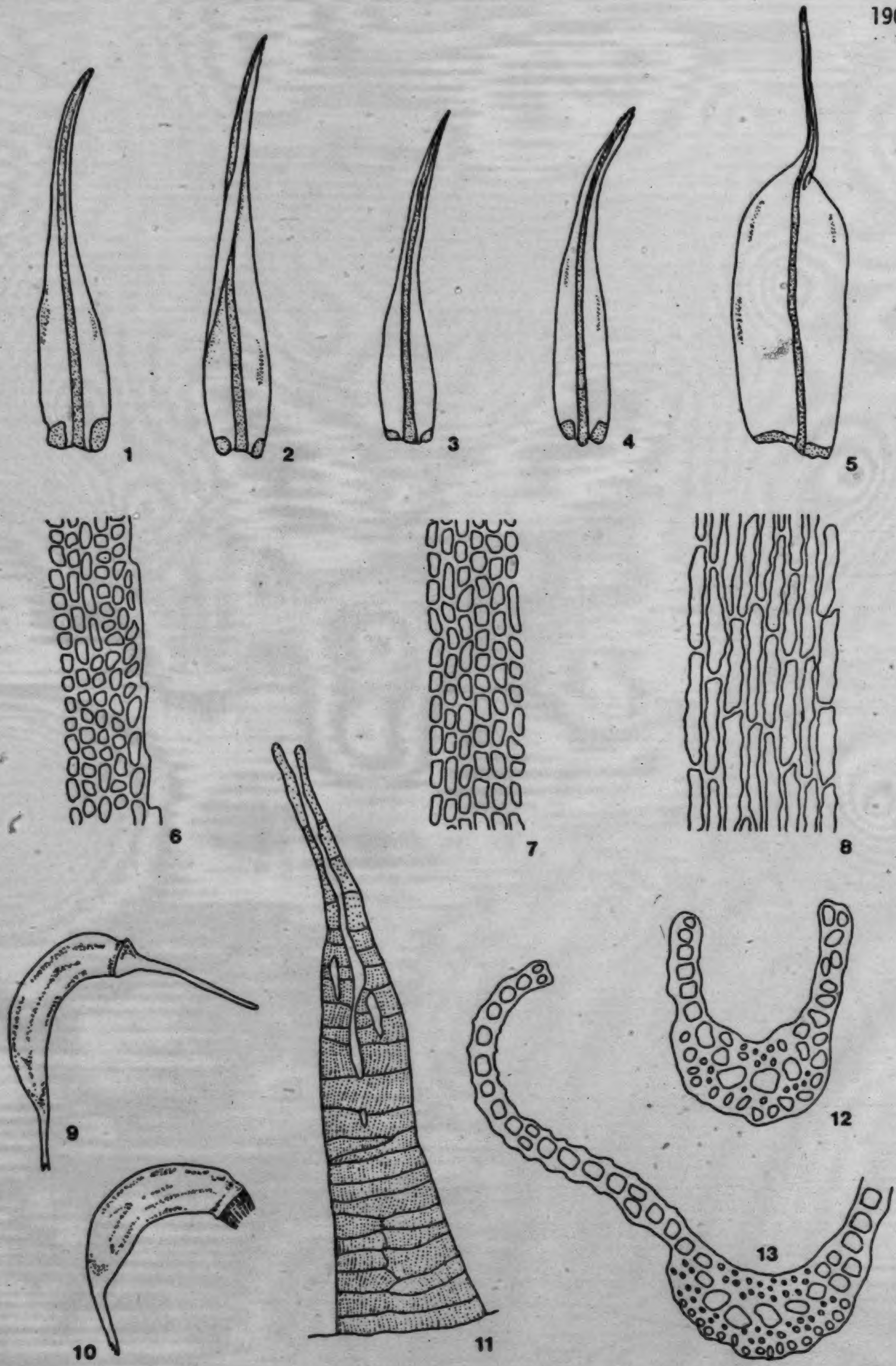
Selected Specimens Cited: EXSICCATI: Lesq. and James, Mosses of N. Amer. 103 (DUKE). Macoun, Can. Musci 588 (US, UC, CANM). Grout, N. Amer. Musci Perf. 259 (UC, CANM). Holzinger, Musci Acroc. Bor. Amer. et Eur. 560 (CANM).

CANADA. Alberta: Banff National Park, Upper Altrude Lake, Frye and Frye 2906 (DUKE). Jasper National Park, Athabasca Glacier, Crum and Schofield 4051 (DUKE). Lake Louise, Macoun 88 (US). Rocky Mtn. House, 52°08'N, 115°26'W, Horton 7226 (ALTA). Ft. McMurray, near Athabasca River about 40 km N of city, Peterson 4680 (ALTA). British Columbia: Fort St. John, Correll 11921 (DUKE). Shushwap Lake, Adam's River, Brinkman 2095 (DUKE). Roger's Pass, Macoun 115 (CANM). Salmon River, Brinkman 388 (US). Lake of Hanging Glaciers, MacFadden 8298 (COLO). Princeton, Flowers 9542 (COLO). Wilmer, MacFadden 259 (UC). Manitoba: Fort Churchill, Twin Lake Hill, Crum and Schofield 7301 (DUKE). Yukon Territory: Onion Lake, 112 km S of Haines junction, Weaver 316 (ALTA). Watson Lake, Correll 12114 (DUKE). Lake Lindeman, Williams May 18, 1898 (F).

FIGURE 39. *Dicranum brevifolium* Lindb. var. *brevifolium*.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Upper transverse-section (280x)
13	Median transverse-section (280x)

190.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U.S.A. Alaska: Haines. 88 km NW along Haines Hw., Hermann 21804 (WTU). Juneau, Juneau Quadrangle, Hermann 22031 (US). 62°40'N 152°30'W, Viereck 5155 (MICH). Colorado: Boulder Co., Lyons, 2100 meters, Weber B-6086 (COLO). San Juan Co., Silverton, Young 24 (MICH). Montana: Flathead Co., West Glacier, Hermann 18221 (F). Lake Co., Yellow Bay, Schofield 11710 (CANM). New Mexico: Taos Co., W slope of Wheeler Peak, Hermann 23969 (CANM).

12b. *Dicranum brevifolium* (Lindb.) Lindb. var. *bistratosum* Ireland *ex* Peterson *var. nov.**

Holotype : Alberta, Banff National Park, Bow Pass. On ground at 2080 meters in elevation. 116°28.5'W, 51°40'N. Beil 103, 1965. (Holotype-ALTA

Paratypes: Jasper National Park, Sunwapta River, N edge of Columbia Icefield. Turner 11427 (ALTA). Banff National Park, Spray River, Biel 354 (ALTA). Yukon Territory, Southern Wernecke Mtns., 64°37'N, 136°46'W, Horton 2695 (ALTA).

Plantae in tegites vel caespites, usque ad 5 cm altae, atrovirides, crescens solia vel homos. Folia sicca torta vel crispa, non undulata, 4.0-7.0 (8.5) mm longa, lanceolata, acuta, apices versus bistrata marginibus integris ad serrulatus, bistratus vel tristratus; costa lata, percurrente ad excurrente. Capsulae obscuro-fuscae, curvae,

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*To be validly published at a later date.

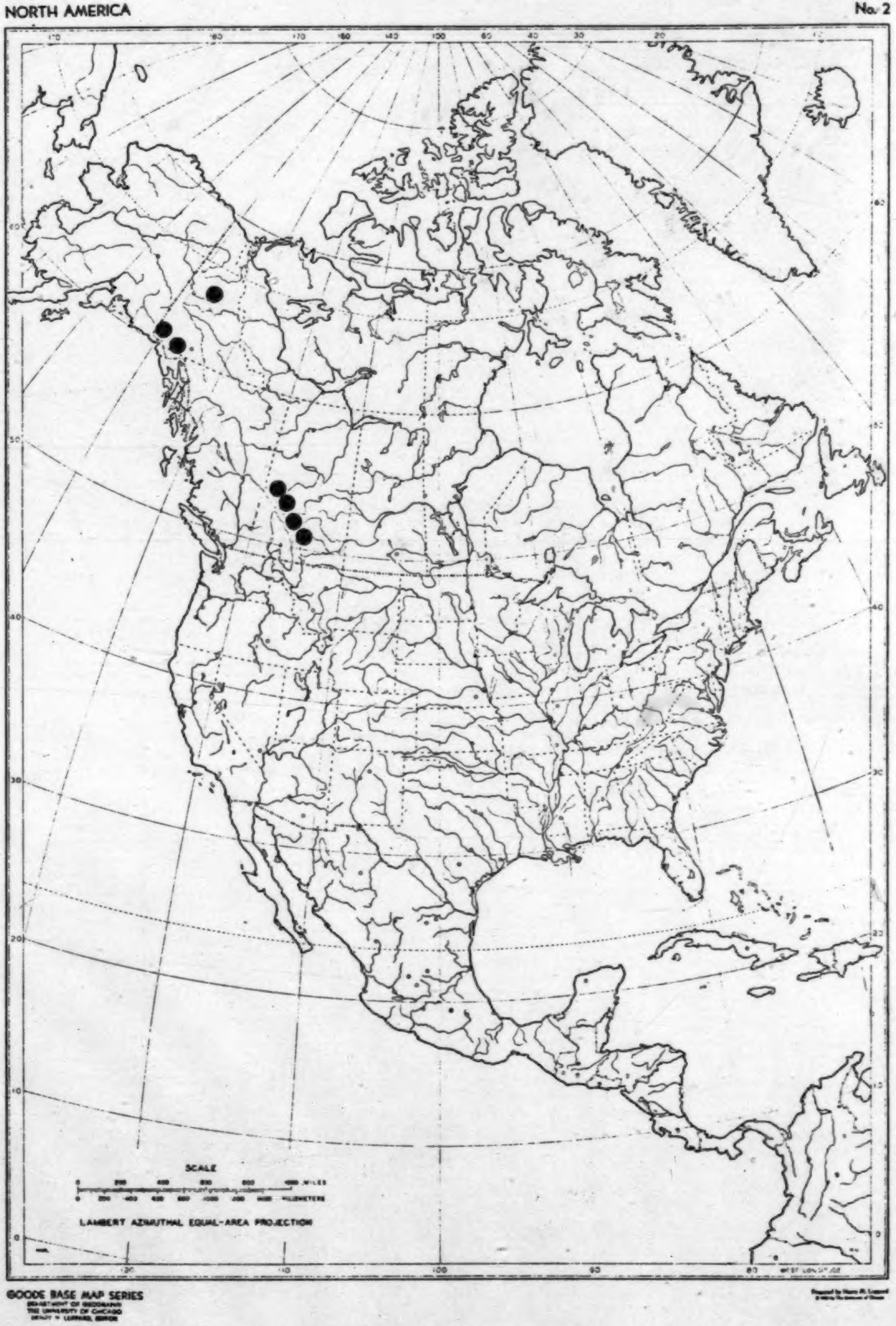
striatae, non strumosae; collorum longorum; dentes peristomii atrorubri, striati; membranae basales saepe adsunt. Sporae (18) 20-26 (29) µm. n=24

Plants in dense mats or tufts, up to 5 cm tall, dark-green sometimes almost black, growing on soil or humus. Stems densely tomentose, tomentum brown to orange and matted. Leaves when dry curled or crisped, rarely falcate-secund, when moist usually straight and spreading, often arching away from stem at right angles, sometimes falcate-secund, not undulate, 4.0-7.0 (8.5) mm long, lanceolate, broad, at the base, tip sharply acute, strongly keeled at least in upper 1/2, not papillose, but cell walls strongly protruding to give appearance of papillae or ridges; margins entire or serrulate, bistratose, tristratose, or rarely unistratose in upper 1/4; costa wide, 150-170 (185) µm just above alar region, percurrent or slightly excurrent, slightly toothed on abaxial surface, in median cross-section showing 6 to 8 guide cells and 2 moderately developed stereid bands, both bands extending well into the apex, each band consisting of 2 cell layers, the abaxial layer of external cells slightly differentiated from stereids by larg lumens, the adaxial layer not differentiated; alar cells brown, bistratose, thin-walled, not reaching costa; basal cells above alar region short-rectangular, smooth or slightly pitted, thin- or thick-walled, 20-60 (75) µm long; median cells short-rectangular to quadrate, corners usually rounded, in fairly uniform rows, extending to within 10 or 15 cells of the leaf base, (6) 10-15 (25) μm long, cell walls strongly bulging; upper cells similar to median, usually completely bistratose, or at least bistratose in spots. Perichaetial leaves shorter than stem leaves, the innermost ones abruptly narrowed to a subulate tip.

Dioicous, male plants as large as female plants. Monosetous, setae brown, 1.5-2.5 cm long. Capsules dark-brown, 2.5-3.5 mm long, curved, lightly ribbed, not strumose, neck long; exothecial cells rectangular, thin- or thick-walled, slightly pitted; stomates 5 to 8 in one row at base of capsule, 36-39 μm long. operculum rostrate, 1.5-2.0 mm long; annulus of 1 or 2 rows of large, thick-walled, hyaline cells; peristome teeth dark-red, vertically striate, ±0.5 mm long, 75-90 μm wide at base, divided half way down into 2 or 3 segments, basal membrane often present. Spores papillose, (18) 20-26 (20) μm. Chromosome number, n=24.

Habitat and Distribution (Fig. 40): This variety has, at present, been collected only in Alberta and the Yukon Territory and it is apparently endemic to western North America. It should be expected in British Columbia and possibly in the Rocky Mountains of Montana. The specimens that have been collected indicate that the habitat is similar to that of *D. brevifolium* var. *brevifolium* which is on soil or humus, often in rocky areas that are well lighted, and at higher elevations of the upper montane.

FIGURE 40. The known distribution of *Dicranum brevifolium* var. *bistratosum* Peterson and Ireland


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
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WEST LONGITUDE
GOODE BASE MAP SERIES
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THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

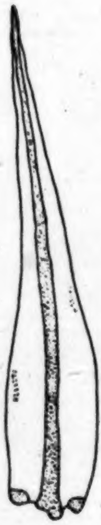
Selected Specimens Examined: CANADA. Alberta: Jasper National Park, 1.6 km S of Pyramid Creek, Stringer, June 21, 1965 (ALTA). Jasper National Park, Old Horn Mtn., Beil, s.n., 1965 (ALTA). Bow River Watershed, Elk Pass Road, just S of Kananaskis Road, Bird and Seaborn 9606 (CANM). Banff National Park, Panther Falls, Bird 8731 (DUKE). Lake Louise, Macoun 21a (US). Yukon Territory: Kluane National Park, Bates Lakes, Douglas 8484 (ALTA).

Dicranum brevifolium var. *bistratosum* differs from *D. brevifolium* var. *brevifolium*, in addition to the bistratose nature of the upper lamina, by occasional tristratose laminal margins, tomentum that is somewhat thicker and leaves that arch away from the stem at right angles. Also, the peristome has a short basal membrane (Fig. 41-11) and chromosome number is n=24 as opposed to that of n=12 in the variety *brevifolium*.

All of the morphological difference are extremes of states found in *D. brevifolium* var. *brevifolium* and there is intergradation between the two. The variety *brevifolium* has occasional bistratose areas in the upper lamina while the variety *bistratosum* has leaves that are generally completely bistratose although occasionally, there are unistratose areas present. The margins are, for the most part, unistratose in the variety *brevifolium* and bistratose in the variety *bistratosum* although each state may be found in either variety. The tristratose margin that is occasionally found in the variety *bistratosum* has not been seen in the variety *brevifolium*. The

FIGURE 41. *Dicranum brevifolium* var. *bistratosum* Peterson and Ireland

1-4	Stem leaves (14x)
5	Perichaetial leaf (280x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth and basal membrane (180x)
12	Upper transverse-section (280x)



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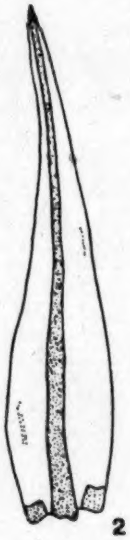

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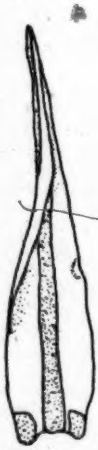

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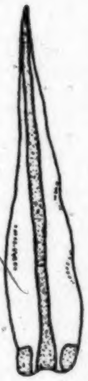

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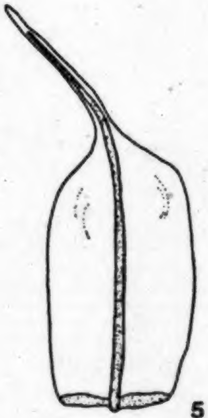

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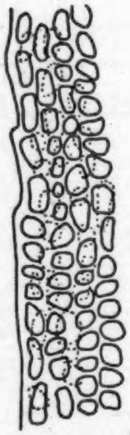

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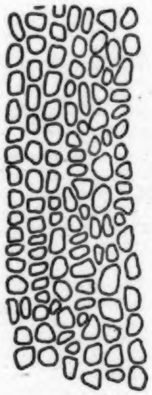

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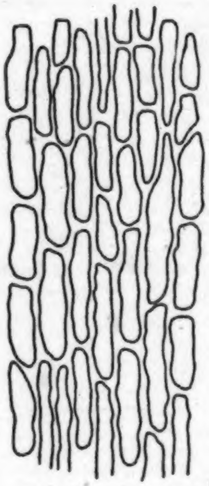

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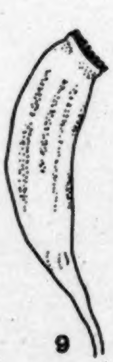

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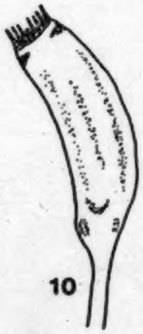

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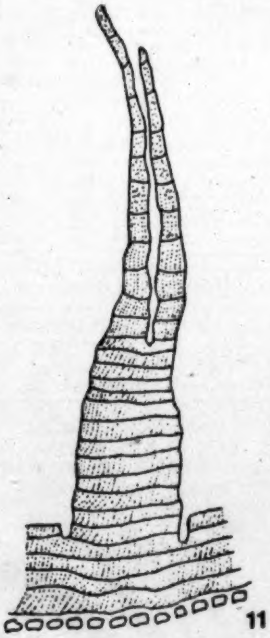

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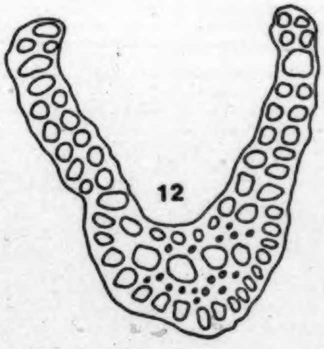

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tomentum is thick along the stems of both varieties but it does seem to be somewhat thicker on the variety *bistratosum*; also, the tomentum appears to enhance the leaf's divergent angle from the stem. That is, the stems with the thicker tomentum have leaves that diverge from the stem at angles somewhere around 90° and those stems with less tomentum have leaves that diverge at lesser angles.

The single distinguishing sporophytic character, the basal membrane of the peristome, has not been seen in the variety *brevifolium* and it was seen in only two specimens of the variety *bistratosum* (the only two with sporophytes) and it is possible that this character state is not consistent.

The polyploid condition of the variety *bistratosum* along with the other morphological differences provide adequate reasons for separating this taxon from the variety *brevifolium*. It is possible that additional collections will reveal other differences or enhance those already noted and the taxon could then be given the status of species. Due to the lack of additional material and the intergradation seen, I choose to recognize this new taxon at the level of variety.

Section: *Elongata* Hag., K. Norsk. Vid. Selsk. Skrift. 1914(1): 140. 1915

Lectotype: *Dicranum elongatum* Schleich. *ex* Schwaegr.

Plants up to 8 cm tall. Leaves not undulate, usually erect and imbricate, lanceolate, apex acute to obtuse; upper lamina cells elongate and pitted or short and smooth, walls between upper cells thick (distance between cells usually > than width of cell lumen); median transverse-section of costa showing one row of guide cells and 2 stereid bands, lumens of stereids small (< 1/2 the wall thickness). Capsules curved to straight, ribbed, neck short; annules present.

13. *Dicranum elongatum* Schleich. *ex* Schwaegr., Spec. Musc. Suppl. 1(1): 171. 1811.

Type: "*Legit in monte Touly ad terran, Schleicher*" (Holotype-G!)

Dicranum sphagni Wahlenberg, Fl. Lapp. 337: 1812. *Hom. illeg. inc. species prior.*

Dicranum subflagellare Card. et Thér., Proc. Wash. Acad. Sci. 4: 298. 1902.

Type: "Kodiak, Trelease, 1899" (Isotype-S!).

Plants in compact tufts or mats up to 6 cm tall, light-green, growing on soil or peat, often among *Sphagnum* species. Stems moderately tomentose, tomentum brown to red. Leaves when dry erect, imbricate, sometimes twisted, when moist erect and imbricate, not undulate, 3-6 (7.5) mm long, narrowly lanceolate, tapering to a sharply acute apex, slightly keeled in upper 1/2 to 1/3, smooth on both surfaces; margins unistratose, entire; costa narrow, 80-95 (110) μm wide just above alar region, percurrent or slightly excurrent, smooth, costa in median transverse-section showing 5 to 7 guide cells and 2 weak stereid bands, both bands extending into upper 1/3 of leaf, neither abaxial layer nor adaxial layer of external cells differentiated from stereid cells; alar cells brown, thin-walled, not extending to costa; basal cells above alar region elongate to linear, 25-40 (55) μm long, very thick-walled, pitted; median cells similar to basal cells, 20-30 (45) μm long; upper cells short, rectangular, 10-15 μm, corners rounded, walls very thick, smooth. Perichaetial leaves shorter than stem leaves, abruptly narrowed to a subulate tip.

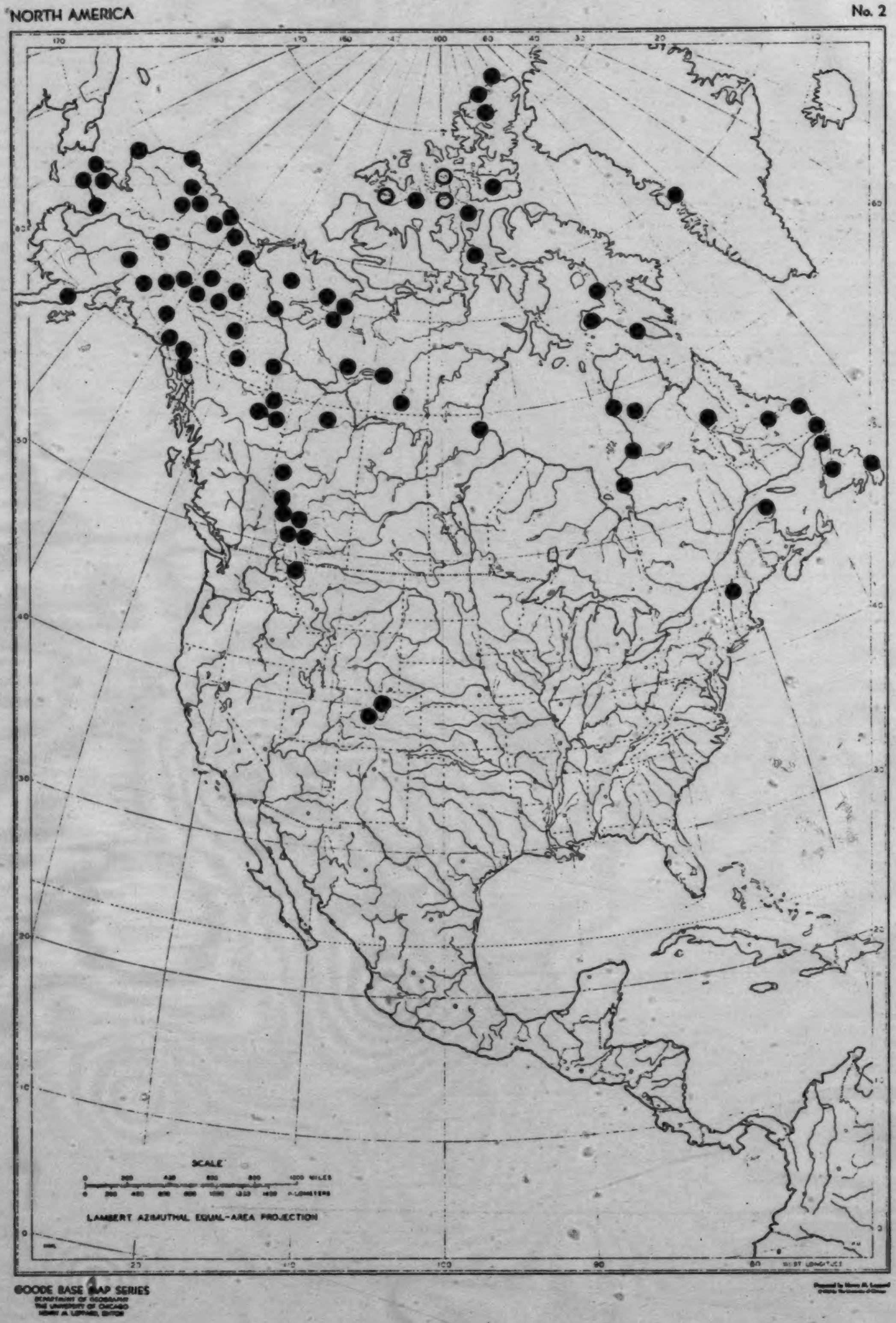
Dioicous, male plants similar to or slightly smaller than female plants and usually intermixed with them. Monosetous, setae single, yellow to brown, 1.2-2.5 cm long. Capsules light-brown, 2.0-2.5 mm long, curved, ribbed, not strumose, neck short; exothecial cells rectangular, thin-walled, not pitted, about 70 μm long; stomates few in one row at base of capsule, 35-40 μm; opercula rostrate, about 1.5 mm long; annulus of 2-3 rows of large thick-walled, hyaline cells; peristome teeth orange to red, vertically striate, about 0.4 mm long, 75-80 (95) μm wide at base, divided about half way down into 2 segments; spores papillose, 18-23 µm. Chromosome number, n=12.

Habitat and Distribution (Fig. 42): *Dicranum elongatum* is the most common member of the genus in arctic regions, and is not uncommon in alpine tundra areas of the Rocky Mountains. It occurs from Alaska eastward across arctic and subarctic Canada into Labrador and the Gaspé region of Quebec. It has been collected as far south as Colorado in the west, and New Hampshire in the east. Specimens are usually found growing in dense, compact tufts or mats in open tundra or rocky habitats, occasionally forming extensive carpets covering up to 50 meters across. In many cases it is found growing with numerous strands of the liverwort *Anastrophyllum minutum* (Schreb. *ex* Cranz) Schust. intermixed in the mat.

Selected Specimens Examined: EXSICCATI. Austin , Musci Appal. 471 (CANM). Holzinger, Musci Acroc. Bor. Amer. et Eur. 599 (CANM), 633 (UC, MICH, CANM). Macoun, Can. Musci 592 (UC, CANM). Drummond, Musci Amer. (Rocky Mtns.) 91 (MICH), 92 (MICH, CANM). Sull. and Lesq., Musci Bor. Amer. (ed. 1) 63 (MICH). Sull. and Lesq., Musci Bor. Amer. (ed. 2) 79 (MICH). Renauld and Cardot, Musci Amer. Sept. 358 (MICH, CANM).

CANADA. Alberta: Banff National Park, Frye 79 (CAS). Jumping Pound Creek, Macoun 107c (DUKE). Jasper, Tonquin Valley, MacFadden 633 (UC). Jasper National Park, Crum and Schofield 5091 (MICH). Jasper National

FIGURE 42. The North American distribution of *Dicranum elongatum* Schleich.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0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
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Jasper National Park, Signal Mtn., 52°53'N, 117°58'W, Peterson 3644 (ALTA). Mountain Park Area, Cardinal River Recreation area, Peterson 878 (ALTA). British Columbia: Beavermouth, Taylor 219 (UC). 58°38'N, 124°40'W, Correll 12037 (MICH). Summit Lake, 160 km W of Ft. Nelson, Peterson 2992 (ALTA). Newfoundland: Labrador, Black Head, Cartwright, Wickes, July 15, 1940 (DUKE). Labrador, Northwest River, Wickes, July 25, 1938 (US). St. John, Bard Harbour Hill, Long 559 (MICH). Quebec: Mt Logan, Collins 5672 (DUKE). Hudson Bay, Great Whale River, Marr M406 (MIN). Port Harrison, Polunin 1687b (MICH). Gerin Mtn., 55°04'N, 67°14'W, Viereck 725 (DUKE). Northwest Territories: Ward Hunt Island, 83°05'N, 75°00'W, Brassard 4405 (TENN). Baffin Island, Lake Harbor, 63°N 70°W. Oldenburg July 23, 1939 (MIN). Small Tree Lake, 61°N, 105°W, Maini 10 (CANM). Great Bear Lake, Steere 10484 (DUKE). Baffin Island, Cape Dorset, Polunin 2381a (MICH). James Bay, South Twin Island, Doutt 2342 (MICH). Norman Wells, 65°15'N, 126°34'W, Jasieniuk 2356 (ALTA). Yellowknife, 62°32'N, 113°21'W, Jasieniuk 2295 (ALTA). Devon Island, Truelove Lowland, Peterson 2542 (ALTA). Yukon Territory: Firth River Basin, 68°40'N, 141°W, Sharp MC58107 (TENN). Dawson, 30 km W of ferry, Peterson 1420 (ALTA). Dempester Hw., 71 km up Highway, Peterson 1610 (ALTA). Mt. Klotz, about 150 km N of Dawson, Peterson 1685 (ALTA).

U.S.A. Alaska: Richardson Hw., Mile 208 (333 km), Lutz 50-300 (DUKE). Brooks Range, Mooney Lake, Jordal 2312 (DUKE). Mt. McKinley National Park, Viereck 3056 (LAF). Romanzof Range, Shushan B1994 (UC).

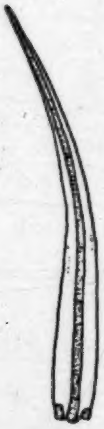
Wainwright, 75 km S of, Shushan and Thompson B172 (LAF). Bering Strait Dist., 68°05'N, 165°32'W, Johnson *et al.* 363 (COLO). Dry Creek, 63°53'N, 147°20'W, Viereck and Jones 5922b (COLO). Colorado: Boulder Co., Weber and Dahl B-6977 (US). Clear Creek Co., Mt. Evans, Weber *et al.* B11032 (COLO). Maine: Mt. Katahdin , Collins 2248 (MICH). Montana: Columbia Falls, Williams Aug. 17, 1895 (F). New Hampshire: Mt. Washington, Allen July 12, 1880 (MICH).

Dicranum elongatum is a slender species that occurs quite frequently in the Arctic and alpine areas of North America and it is normally easy to identify because of its habitat, small size, and growth habit of very compact cushions. These character states plus the small capsules are usually more than sufficient to distinguish this species from all other Dicrana except for its close relative *D. groenlandicum*. According to Crum (1973) these tufts are probably what the natives were referring to in Franklin's *Journey to the Polar Sea* (1824) as "Women's Heads" because "when you kick them they never get out of the way".

The major character that distinguishes these two species is the shape of the upper laminal cells. *Dicranum elongatum* has upper cells that are short, about 2 to 1 in length/width ratio with walls that are smooth (Fig. 43-6), while *D. groenlandicum* has long upper cells with a length/width ratio of about 4 to 1 and cell walls that are strongly pitted (Fig. 46-6). Both species have long median and basal cells with pitted walls. Leaf length is slightly greater in

FIGURE 43. *Dicranum elongatum* Schleich.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)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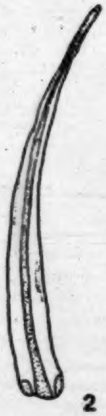
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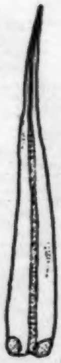
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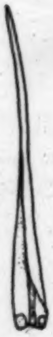
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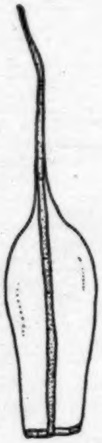
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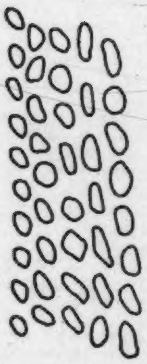
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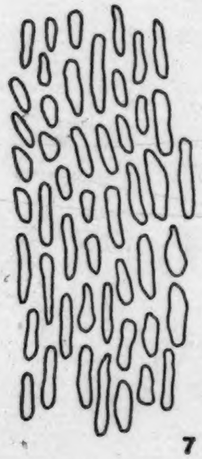
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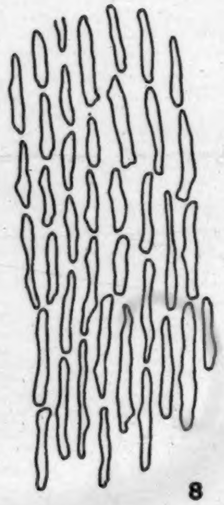
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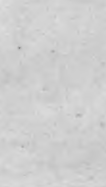
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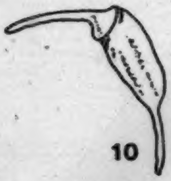
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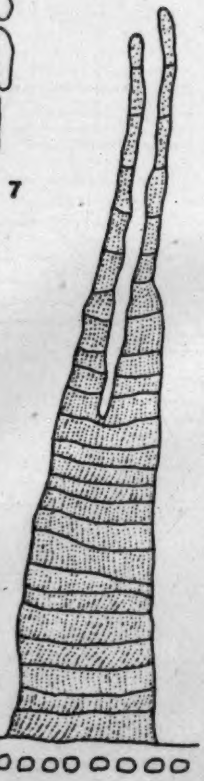
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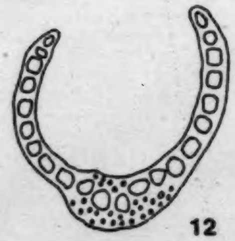
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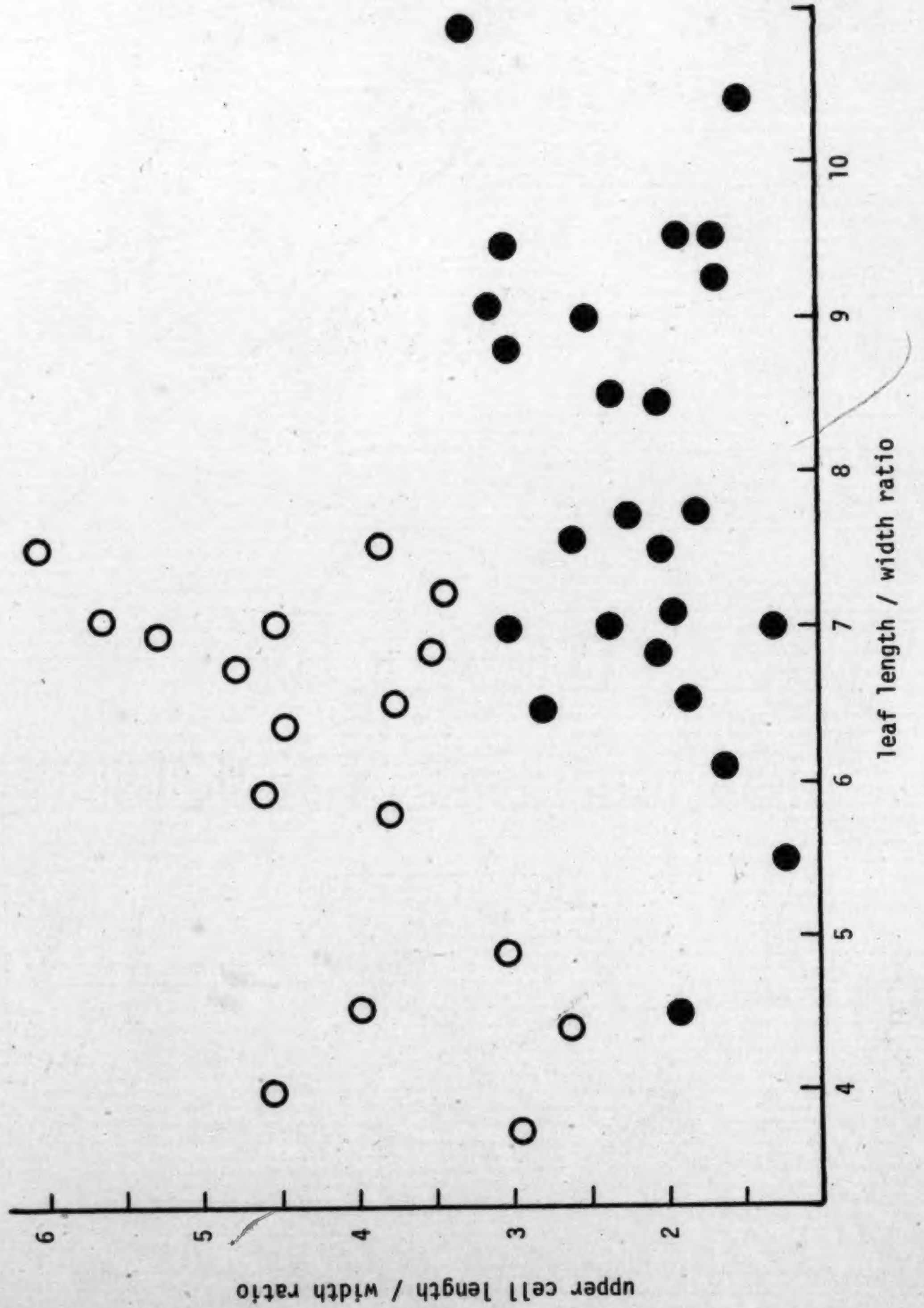
D. groenlandicum although there is considerable overlap in this area. If the leaf length is used in the form of leaf length/width ratio and graphed against the upper cell length/width ratio as seen in Fig. 44. the separation of the two species can be graphically displayed. Although the leaves of *D. groenlandicum* are slightly longer (on the average) than leaves of *D. elongatum*, their length/width ratio is about 6 to 1 while those of *D. elongatum* have a length/width ratio of about 8 to 1. This is due to the narrow nature of the leaves of *D. elongatum* and the shape of the leaf apex. Normally the apex of *D. groenlandicum* is somewhat obtuse with a subpercurrent costa while the apex of *D. elongatum* is strongly acute with a percurrent or slightly excurrent costa. Although this is generally true, and the character state may be used as an aid in separating the two taxa, it is not consistent. Occasionally specimens of *D. groenlandicum* will have acute tips with a percurrent costa. Figure 44 shows that the two species overlap in both leaf and cell length/width ratio when a number of specimens are compared; however, if the additional character of upper cell wall appearance is applied (open circles represent specimens with pitted walls, closed circles represent specimens with smooth walls) concise groups are apparent.

FIGURE 44. A comparison of leaf length/width ratio against upper cell length/width ratio in *Dicranum elongatum* Schleich. and *Dicranum groenlandicum* Brid. Closed circles (●) represent specimens with smooth walled upper cells, and open circles (○) represent specimens with pitted walled upper cells. Each dot represents the mean of five measurements taken from a single population.


leaf length / width ratio
4
5
6
7
8
9
10
upper cell length / width ratio
2
3
4
5
6

14. *Dicranum groenlandicum* Bridel, Musc. Recent. Suppl. 4: 68. 1819.

Type: "... Groenlandia ... Blumbach ..." (Isotype-B!).

Dicranum labradoricum C. Müll., Syn. 1: 366. 1848.

Type: "Labrador: Kurr in hb. Kunzeano." not seen *fide* Williams, 1913.

Dicranum tenuinerve Zett., Sv. Vet. Akad. Handl. II 13: 14. 1876.

Type: "Alten, in monte Store-Reipasfjell ..." (Isotype- UPS!).

Dicranum macounii Austin, Bot. Gaz. 2: 96. 1877.

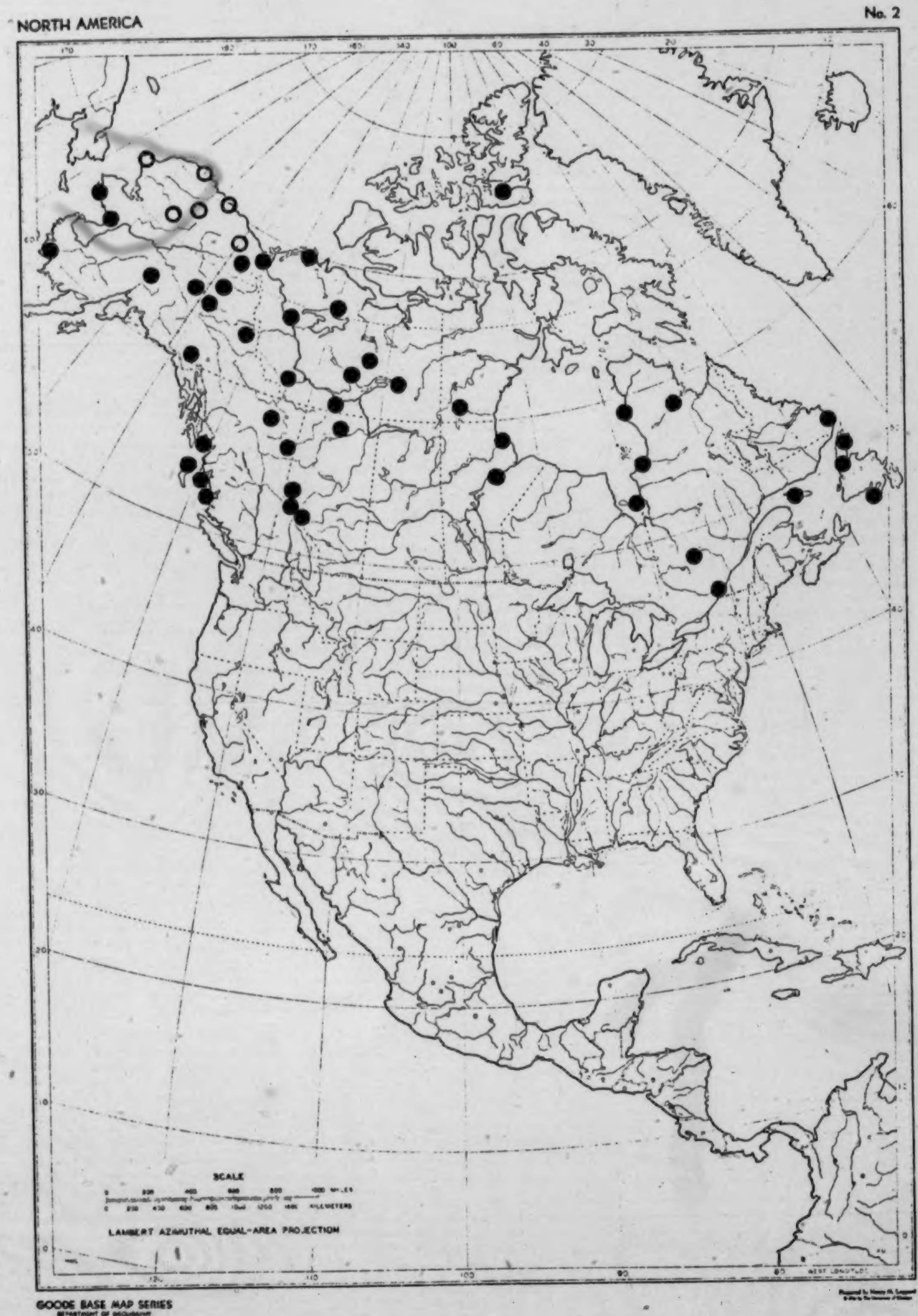
Type: "Peace River, 1871, Macoun." (Lectotype-NY!).

Plants in compact tufts, up to 8 cm tall, light-green, growing on soil. Stems moderately tomentose, tomentum brown to red. Leaves when dry erect and imbricate or rarely slightly falcate-secund, when moist strongly erect and imbricate, not undulate, (3) 4-6 (8) mm long, narrowly lanceolate, tapering to an obtuse or rarely acute apex, slightly keeled in upper 1/2, smooth on both surfaces; margins unistratose, entire; costa narrow 55-70 (85) μm wide just above alar region, subpercurrent or rarely percurrent, smooth, costa in median transverse-section showing 5 to 7 guide cells and two stereid bands, both bands extending into upper 1/3 of leaf, neither abaxial nor adaxial layer differentiated from steried cells; alar cells brown to dark-red, thin-walled, not extending to costa; basal cells above alar region elongate to linear, 45-55 (70) μm long, very thick-walled, pitted; median cells similar to basal cells, 25-40 (45) μm long; upper cells elongate, very thick-walled, pitted, 25-35 (45) μm long. Perichaetial leaves shorter than stem leaves, abruptly narrowed to a subulate tip.

Dioicous, male plants similar to female ones and usually intermixed with them. Monosetous, setae yellow to brown, (0.5) 0.8-1.5 (2.5) cm long. Capsule yellow to light-brown, 1.5-2.5 mm long, straight or rarely slightly curved, ribbed, not strumose, neck short; exothecial cells rectangular, thin-walled, not pitted, 45-60 μm long; stomates few in one row at base of capsule, 27-30 (33) μm long; opercula rostrate, about 1.5 mm long; annulus of one to three rows of large, thick-walled, hyaline cells; peristome teeth red to red-brown, 250-300 μm long, 70-85 μm wide at base, divided about half way down into 2 segments; spores papillose, 19-24 μm. Chromosome number, n=12.

Habitat and Distribution (Fig. 45): The habitat of *D. groenlandicum* is similar to that of *D. elongatum* in that it is commonly found in tundra areas, usually in the more protected areas such as in rock crevices and between hummocks. It occurs from the west coast of Alaska eastward across Canada to the coast of Newfoundland and extends northward as far as the Mackenzie River Delta and Devon Island in the Northwest Territories. Its southern-most limits are around Jasper National Park in the west and southern Ontario in the

FIGURE 45. The North American distribution of *Dicranum groenlandicum* Brid.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No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1600 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard

east. It has not been found in the United States except for Alaska. It is also reported from Greenland (type locality), Scandanavia, across the Arctic into Siberia, and in the Alps.

Selected Specimens Examined: EXSICCATI. Reneauld and Cardot, Musci Amer. Sept. 6 (CANM).

CANADA. Alberta: Jasper National Park, Amethyst Trail, Crum and Schofield 5081 (DUKE). Willmore Wilderness Area, 53°32'N, 118°32'W, Peterson 3455 (ALTA). Jasper National Park, Signal Mtn., Peterson 3672 (ALTA). British Columbia: Queen Charlotte Is., Graham Is., Tow Hill, Schofield and Krajina 39376 (UBC). Summit Lake, about 160 km W of Ft. Nelson, Peterson 2996 (ALTA). Calvert Is., Schofield and Williams 27113 (DUKE). Manitoba: Churchill, Eskimo Point, Crum and Schofield 7169 (DUKE). Newfoundland: Labrador, Battle Harbor, More 1898 (US). Gros Morne National Park, 49°42'N, 57°56'W, Bouchard and Hay June 20, 1972 (CANM). 51°33'N, 55°53'W, Tuomikoski 3471 (MICH). Ontario: Ottawa Dist., Mer Bleue, Macoun Aug. 12, 1803 (CANM). Quebec: Leaf River, 58°05'N, 72°40'W, Marr 89a (DUKE). Port Harrison, Polunin 1672a-2 (MICH). Anticosti Island, Jupiter River, Macoun Aug. 20 1883 (CANM). Hudson Bay, Great Whale River, Brisson and Forest 397 (CANM). Northwest Territories: Richardson Mtns., 68°04'N, 135°25'W, Krajina 63071173 (DUKE). Ft. Enterprise, 64°28'N, 113°10'W, Plath Aug. 1, 1970 (SMS). Mackenzie River Delta, W of Anderson River, Scotter 5049 (CANM). Norman Wells, Peat Plateau, 65°14'N, 127°04'W, Jasieniuk 2328 (ALTA). Yellowknife, Ingraham Trail, Jasieniuk 2287 (ALTA). Devon Is., Truelove Lowland, Peterson 2549 (ALTA). Yukon Territory: Dawson City, Bonanza Creek, Macoun July 18, 1902 (DUKE). Wernecke Mtns., 64°30'N, 135°06'W. Scotter 17973a (C). Mt. Klotz area, about 150 km N of Dawson City, Peterson 1689 (ALTA).

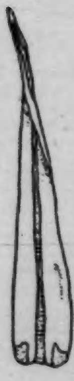
U.S.A. Alaska: Annette Is., Eyerdam, Sept 24, 1951 (DUKE). Wonder Lake, 63°28'N, 150°55'W, Weber and Viereck 10328 (UC). St. Michael, Setchell 49 (UC). Bethel, Yorke 6644 (F). Seward Peninsula, Kuzitrin Lake, Sigafoos 1501 (MICH). Upper Salcha River, 64°40'N, 144°15'W, Johnson 57 (CANM).

Dicranum groenlandicum is a species with an arctic and alpine distribution that is quite similar to *D. elongatum*. The two species are closely related and grow in similar habitats and normally, microscopic characters must be examined to separate them. *Dicranum groenlandicum* has pitted walls of the upper cells (Fig. 46-6) while *D. elongatum* has smooth walled upper cells (Fig. 43-6). This character is supported by leaf and cell length width ratios (See Fig. 44 and Discussion under *D. elongatum*).

When mature sporophytes are present they can also be used to distinguish the two species. All species of *Dicranum*, except *D. groenlandicum* and *D. rhabdocarpum*, have curved capsules. Those of *D. groenlandicum* are rarely slightly curved; generally they are

FIGURE 46. *Dicranum groenlandicum* Brid.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (280x)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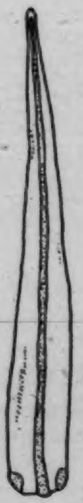
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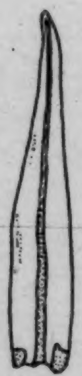
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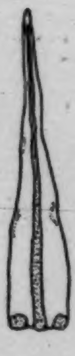
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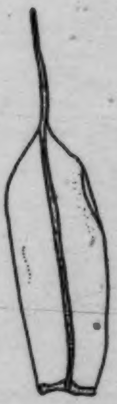
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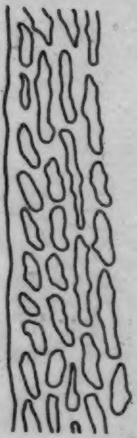
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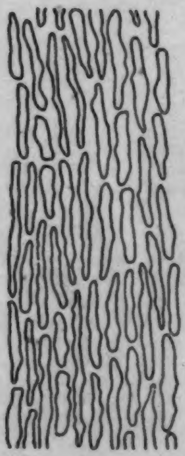
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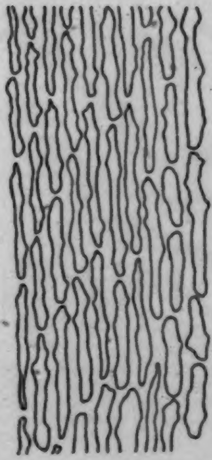
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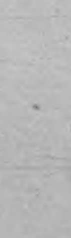
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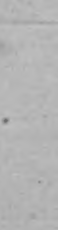
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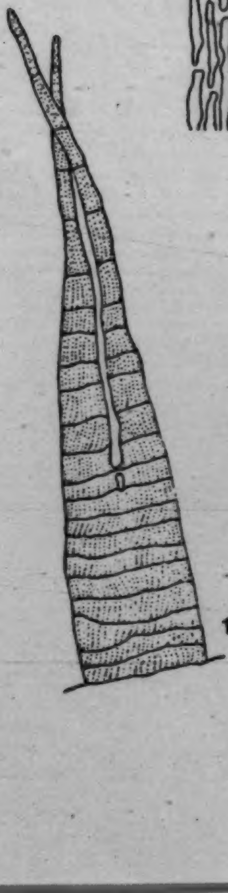
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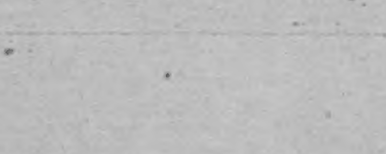
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straight (Fig. 46-9) and quite different from the curved capsules of *D. elongatum* (Fig. 43-9), although they are similar in size. This straight or erect state might suggest that the species belongs in the segregate genus *Orthodicranum*; however, *D. groenlandicum* has ribbed capsules, bistratose alar cells, and a habitat of soil. All of these character states are found in the genus *Dicranum*, not *Orthodicranum*. In addition, its closest relative, *D. elongatum*, is a species with curved capsules and unquestionably a member of the genus *Dicranum*.

Section: *Spuria* B.S.G., Bryol. Eur. Fasc. 37-40. 1: 118. 1847.

Lectotype: *Dicranum spurium* Hedw.

Plants up to 14 cm tall. Leaves undulate, falcate-secund to erect and imbricate, lanceolate to ovate-lanceolate, apex acute to obtuse; upper lamina cells short-rectangular to triangular, sometimes wider than long, arranged in loose irregular rows; median transverse-section of costa showing one row of guide cells and 2 stereid bands, lumens of stereids small (< 1/2 the wall thickness). Capsules curved, ribbed, neck short; annulus present.

15. *Dicranum condensatum* Hedw., Spec. Musc. 139. 1801. *non* plate 34.

Type: *"Locus terrestris, circa Lancaster Pensilvaniae lectum a* Rev. D. Muehlenberg." (Holotype-G!)

Dicranum sabuletorum Ren, et Card., Rev. Bryol. 15: 701. 1888.

Types: "Sull. and Lesq., Musci Boreali Americani exsicc. Florida (Fitzgerald, Sawyer). Louisiana (Langlois). Carolina (H.A. Green)." Isosyntypes: Sawyer (MIN! US! MICH!), Green (NY!).

Dicranum arenarium Ren. et Card., Rev. Bryol. 15: 70. 1888. *nom. nud.*

Cecalyphum condensatum (Hedw.) P. Beav., Prodr. 50. 1805.

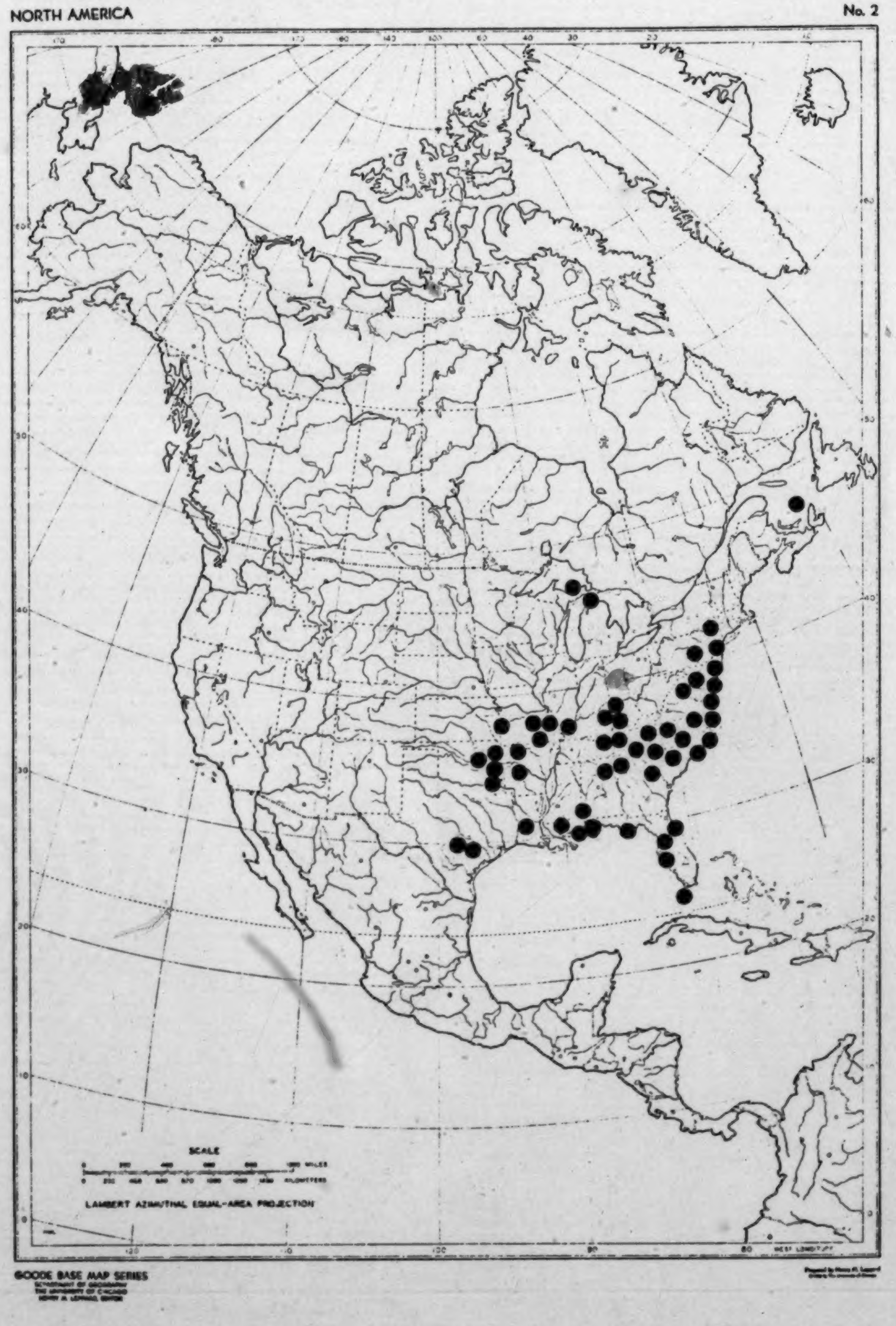
Plants small to medium, up to 6.5 cm tall, in loose to dense mats, light-green, usually growing on sandy soil. Stems moderately tomentose, tomentum light- to dark-brown. Leaves when dry strongly crisped or rarely only falcate-secund, when moist straight or falcate-secund and imbricate, slightly undulate, (2.0) 3.5-6.5 (8.0) mm long, gradually tapering to a sharply acute apex, widest at or near the base, keeled in upper 1/3, upper 1/4 very twisted, lamina papillose on abaxial surface or rarely smooth; margins serrate to entire, unistratose; costa narrow, 90-110 (125) µm wide just above alar region, percurrent or often slightly excurrent, strongly toothed on abaxial side in upper 1/4, papillose farther down, costa in median transverse-section showing 6 to 8 guide cells and 2 well developed stereid bands, both bands extending well into the apex, abaxial layer of external cells well differentiated from stereids by large lumens, adaxial layer not differentiated; alar cells usually brown, bistratose, thin-walled, not extending to costa; basal cells just above alar region (40) 60-100 (115) µm long, thick-walled, slightly pitted, with an abrupt change to short-rectangular or triangular median cells, 8.0-15 (22) µm long; upper cells short-rectangular or triangular, not pitted, sometimes wider than long, 5.0-12 (17) µm long, thick-walled, in rather uniform rows; marginal cells similar to median or slightly longer. Perichaetial leaves slightly shorter than stem leaves, the innermost ones abruptly narrowing to a subulate tip.

Dioicous, male plants dwarfed, growing on tomentum of female. Monosetous, setae yellow, (2.) 3.0-4.5 cm long. Capsules curved, bent at a sharp angle where neck joins seta, 1.5-2.5 mm long, slightly ribbed, usually strumose, neck very short; exothecial cells thick-walled and rectangular in middle, quadrate or triangular in neck; stomates few, in one row at base of capsule 26 — 32 μm long; opercula rostrate, 2.0-2.5 mm long; annulus fragmenting, composed of 2 rows of hyaline, thick-walled cells; peristome teeth red, vertically striate, about 0.5 mm long, 60-90 (105) μm wide at base, divided half way down into 2 segments. Spores green to brown, papillose, 18-22 μm. Chromosome number, n=12 (11 + x + y).

Habitat and Distribution (Fig. 47): This distinct species is endemic to eastern North America being found from the Magdalen Islands just north of Prince Edward Island southward as far as the Florida Keys. Its western limits are reached in northern Michigan, eastern Oklahoma and southeastern Texas. The normal habitat of *D. condensatum* is sandy, well drained soil, usually in such open areas as pine forests. It may occasionally be found growing in dense woods and may be found in association with *D. spurium* in such cases. Poorly developed plants are sometimes found on thin soils over rocks.

The northern limit of the continuous distribution pattern of this species extends through Arkansas, along the northern Kentucky border and northward through Virginia and Pennsylvania into southern New York. The most northern localities of northern Michigan and the Magdalen Islands represent specimens from either

FIGURE 47. The known distribution of *Dicranum condensatum* Hedw.


NORTH AMERICA
No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
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proposed refugial areas or, in the case of the Magdalen Islands, areas partially surrounded, but not covered by the ice (Prest, 1969). In these disjunct localities the species was collected on sandy soil in "pine barrens".

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 96 as *D. spurium* var. (NY, FH, CANM). Drummond, Musci Amer. (Rocky Mtns.) 48 as *D. congestum* (DUKE). Grout, N. Amer. Musci Perf. 158 as *D. pallidum* (FH, DUKE, MICH, UTAH, CANM). Holzinger, Musci Acroc. Bor. Amer. 54 as *D. sabuletorum* (NY, MICH, CANM, DUKE), 533 as *D. bergeri* (NY, CANM). Macoun, Can. Mosses 1908a series, 24a as *D. pallidum* (FH). Renauld and Cardot, Musci Amer. Sept. 9 as *D. sabuletorum* (FH, MICH). Small, Mosses of Southern U.S. 33 (DUKE, CANM). 36 as *D. pallidum* (FH, NY, CANM, US). Sull., Musci Allegh. 160 (NY, FH, MICH). Sull. and Lesq., Musci Bor. Amer. (ed. I) 68 (NY, US), 68b as *D. spurium* var. (MIN, US, MICH, NY). Sull. and Lesq., Musci Bor. Amer. (ed. II) 85, 85 as *D. spurium* var. (MIN, MICH, NY).

CANADA. Quebec: Magdalen Islands, Alright Is., Reilly 687 (CANM).

U.S.A. Arkansas: Garland Co., Hot Springs National Park, Demaree 22736 (DUKE). Saline Co., Alum Fork, W of Benton, Anderson 11304 (DUKE). Alabama: Dekalb Co., Little River Canyon, Lampton 1639 (DUKE). Baldwin Co., Gulf State Park, Webster and Wilbur 776 (DUKE).

Mobile Co., 6.4 km E of Citronelle, Webster and Wilbur 760 (DUKE). Florida: Gulf Co., Port St. Joe, Schornherst, Mar. 15, 1940 (DUKE). Franklin Co., Dog Island, Reese 753 (DUKE). Marion Co., Ocala National Game Refuge, Wilbur and Webster 2675 (DUKE). Florida Keys, Big Pine Key, Small *et al.* 3666 (MICH). Georgia: Lincoln Co., 6.4 km SW of Lincolnton, Wilbur and Webster 2787 (MICH). Lincoln Co., 4.8 km S of Standford, Wharton 1762 (MICH). Louisiana: Sabine Co., 6.4 km NW of Hornbeck, Reese 9352 (US). Washington Co., 2.4 km N of Vernado, Reese and Thieret 7737a (US). Maryland: Silva, vicinity of Salisbury, Smith 69 (CANM). Michigan: Alger Co., Pictured Rocks, Steere 589 (MICH). Emmet Co., Bit Stone Bay Nichols 392 (MICH). Missouri: St. Genevieve Co., Pickle Springs, 1.5 km E of Farmington, Peterson 3329 (ALTA). Wayne Co., Williansvelle, Russell 23 (MICH). Mississippi: Harrison Co., E end of Ship Island, Reese 3154 (US). New Jersey: Mammouth Co., Lakewood, Small 3128 (CANM). New York: Greene Co., 2.6 km E of of Palenville, Smith 20229 (CANM). North Carolina: Burke Co., Bennett Mem. Park, Peterson, May 8, 1975 (ALTA). Nash Co., 2.4 km E of Middlesex, Anderson 3635 (DUKE). Oklahoma: Delaware Co., Dripping Springs, Redfearn 20962 (SMS). Leflore Co., 2.4 km W of Broken Bow, Redfearn 19882 (LAF). Pennsylvania: Dauphin Co., Small Nov. 1, 1892 (LAF). South Carolina: Fairfield Co., 16 km W of Winnsboro, Culberson 7549 (DUKE). Lancaster Co., Near 40 acre Rock, Stimson 4418 (DUKE). Tennessee: Knox Co., New Hopewell, Sharp 34839 (MICH). Putnam Co., Monterey, Sharp 3699 (CANM).

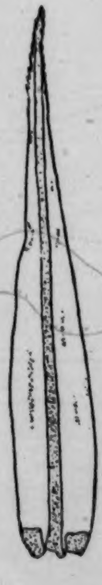
Seview Co., Bruchy Mt., Sharp 3548 (MICH). Texas: Near Harward, Grout Feb. 1931 (DUKE). Virginia: Orange Co., 6.4 km SW of Ruckersville, Ireland 995 (CANM). Cape Henry, near Coles, Leonard and Killys 233 (COLO).

In its typical form *Dicranum condensatum* is readily distinguished from all other North American Dicrana by having a twisted compact appearance, solitary setae, capsules that are bent sharply at the connection to the setae, and a habitat of sandy soil. In the sterile or atypical forms, it might be confused with *D. spurium*, *D. ontariense*, or even *D. fuscenscens* and *D. undulatum*. Gametophytically, *D. condensatum* differs from *D. spurium* by its much narrower leaves that diverge from the stem at a much sharper angle and have fewer undulations. From *D. ontariense* it is distinguished by shorter, crisped leaves, weaker serrations on the margins and short marginal cells that seldom exceed 15 µm in length. *D. ontariense* has long falcate-secund leaves with long cells in the margin that often reach 65 µm in length. From *D. fuscescens* it should be easily distinguished by its irregular areolation and short leaves; from *D. undulatum* by its excurrent or percurrent costa and the abrupt change from longer basal cells to shorter median cells.

Nomenclature: This species has been the source of considerable nomenclatural confusion (Peterson, 1977a) because in Hedwig's

FIGURE 48. *Dicranum condensatum* Hedw.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (140x)
12	Median transverse-section (140x)
13	Section of alar cells (140x)



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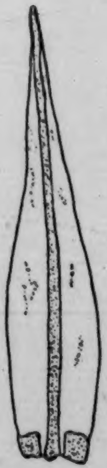

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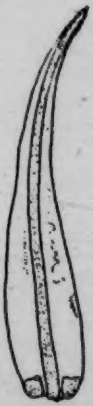

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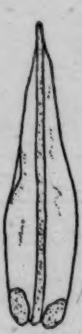

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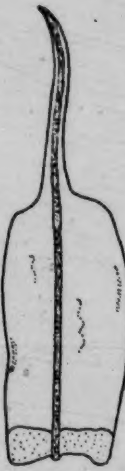

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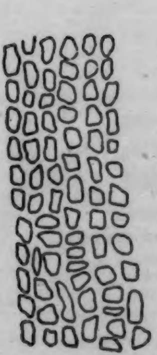

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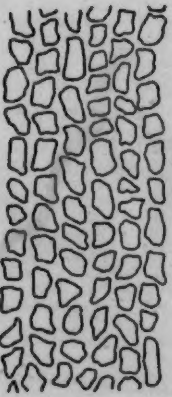

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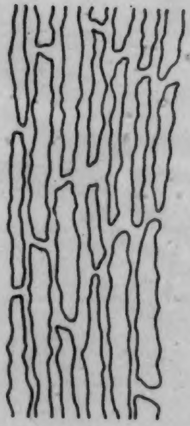

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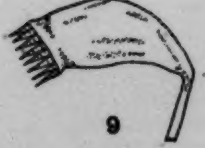

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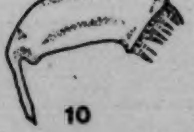

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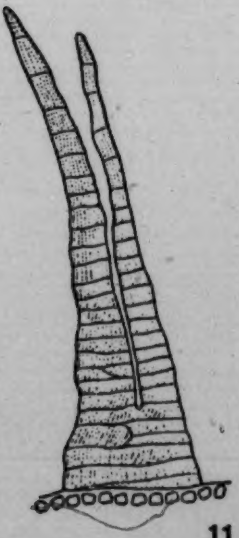

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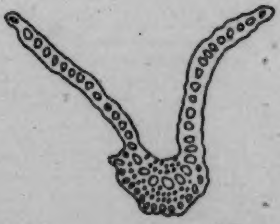

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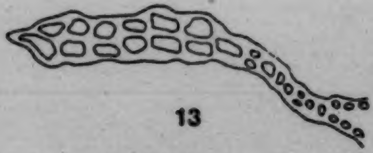


13

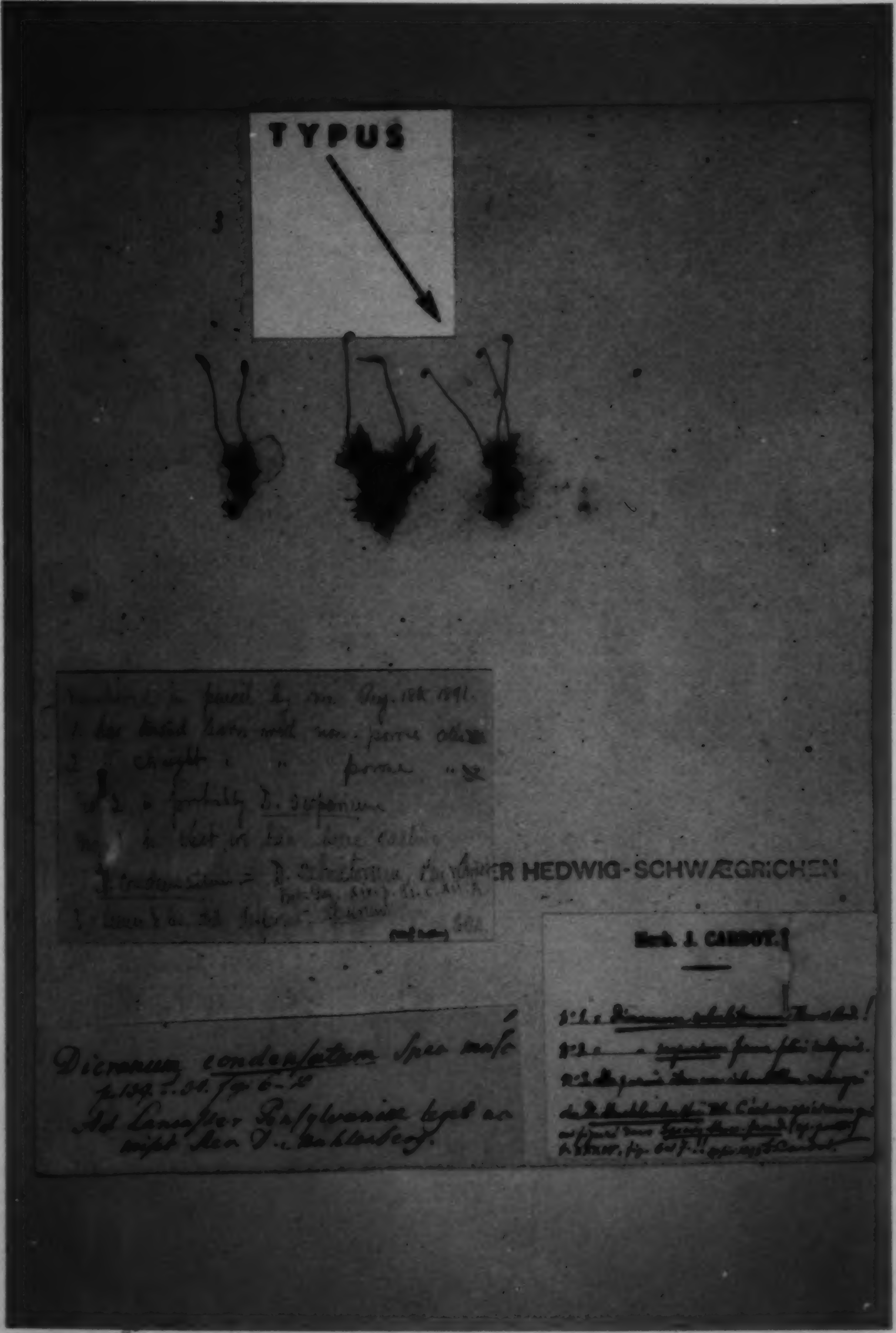
herbarium there are three discordant elements on the type sheet (Fig. 49). Hedwig (1801), in his plate 34 which is labelled *D. condensatum*, drew the specimen to the far left on the type sheet; however, in his description he definitely described the specimen on on the far right of the type sheet. It is the specimen on the left that has caused the confusion and the general acceptance of Renauld and Cardot's name *D. sabuletorum* as correct. In fact, there has been little agreement as to what the specimen on the left actually represents. There is a note attached to the type sheet in the hand of Elizabeth G. Britton stating:

> "Numbered in pencil by me Aug. 18, 1891.
>
> 1. has twisted leaves with non porose cells
> 2. has straight leaves with porose cells
> 2. is probably *D. scoparium*
> 1. is what has been called *D. condensatum* = *D. sabuletorum* Ren. and Cardot Bot. Gaz. XIV. p. 91. t XII A.
> 3. seems to be still different. *spurium*?"

Her numbering starts from the right, so she has referred the confusing specimen on the left to *D. spurium*.

Cardot examined the sheet in 1893 and according to his note attached to the bottom right corner, No. 3 (he used Britton's numbering system) is a small form of *D. muehlenbeckii* B.S.G. He also placed No. 1 under his *D. sabuletorum* which was described in 1888 (Ren. and Card. 1888), and agreed with Britton that No. 2 is

FIGURE 49. Hedwig's type sheet from the Genevé Herbarium with three *Dicranum* species attached. The holotype of *Dicranum condensatum* Hedw. is indicated by the arrow.



TYPUS

[illegible] in pencil by me Aug. 18th 1891.
1. [illegible]
2. [illegible] straight [illegible]
[illegible] probably D. [illegible]
[illegible]
D. condensatum = D. [illegible]
[illegible]

[illegible]ER HEDWIG-SCHWÆGRICHEN

Dicranum condensatum Spec. musc. p. 139 t. 34 fig. 6-[illegible]
Ad Lancaster Pensylvaniae lecta a misit Rev. D. Muhlenberg.

Herb. J. CARDOT.

N° 1. = Dicranum [illegible] !
N° 2. = [illegible]
[illegible]

D. scoparium. The type was examined again by R.S. Williams for his work on the Dicranaceae in North American Flora (1913), and he agreed with both Britton and Cardot as to the determinations of No. 1 and No. 2, but said No. 3 was probably *D. flagellare* because of the ± erect capsules and the smaller cells in the upper part.

In all probability, Renauld and Cardot did not examine the type of Hedwig's *D. condensatum* before describing *D. sabuletorum* since they stated explicitly in their original list of synonymy that *D. condensatum* Hedw. was not included. Eleven years later after examining the type (as evident by Cardot's label on the specimen), Cardot stated that *D. sabuletorum* R. and C. = *D. condensatum* Hedw. (Cardot, 1899). However, he chose to retain the name *D. sabuletorum* stating that Hedwig's concept of the species was poor. He noted that Hedwig said the species was not undulate or crispate (Cardot also said that it is not undulate) and that the plate was not of *D. condensatum* .

I have examined the type sheet and definitely agree as to No. 1 being *D. condensatum* Hedw. = *D. sabuletorum* R. and C., and to No. 2 being *D. scoparium* Hedw. I must agree with Williams on the determination of No. 3. This species has the characters mentioned by Williams plus a unistratose alar region. Both *D. spurium* Hedw. and *D. muehlenbeckii* B.S.G. have bistratose alar regions. Therefore, since *D. flagellare*, *D. scoparium*, and *D. condensatum* are all Hedwigian species, it perhaps should be assumed that he did have a good concept of each! Furthermore, as Williams points out, Hedwig's description of *D. condensatum* states "*Pedunculi pallidi*", and No. 1 is the only specimen on the sheet with yellow setae. No. 2 is eliminated due to lack of an annulus and No. 3 does not have a curved capsule.

It is unfortunate that Hedwig's plate pictures the wrong specimen, but his description definitely circumscribes specimen No. 1 on the type sheet. Also, the three specimens are easily separable, and according to Art. 70 of the International Code of Botanical Nomenclature (Stafleu *et al.*, 1972), No. 1 is a legitimate type. Therefore, a type exists that represents what the author intended according to his description and, in agreement with Williams, there is no reason not to accept *D. condensatum* Hedw. as the the valid name for the species. Hedwig's specimen from the Geneva Herbarium (G), collected in Lancaster, Pennsylvania, by Rev. D. Muhlenberg and placed on the right side of the type sheet (as indicated by the arrow on Fig. 49) is confirmed as the holotype. Hedwig's plate 34 is excluded.

16. *Dicranum spurium* Hedw., Spec. Musc. 141. 1801.

Types: "*In sylvatiens arenosis Ducatus Megapolitani*
Timm, in alpium Sanensium rupestribus Bridel.
In pinetis arenosis Erlangensibus ...".
(Syntype - "Erlang 1796"-G!)

Dicranum brachycaulon Kindb. *in* Macoun and Kindb., Cat. Can. Pl. 6: 34. 1892.

Type: "On dry rocks in open woods near the lighthouse at Yarmouth, N.S., June 23, 1883. (Macoun)". (Lectotype-CANM!; Isotype-NY!).

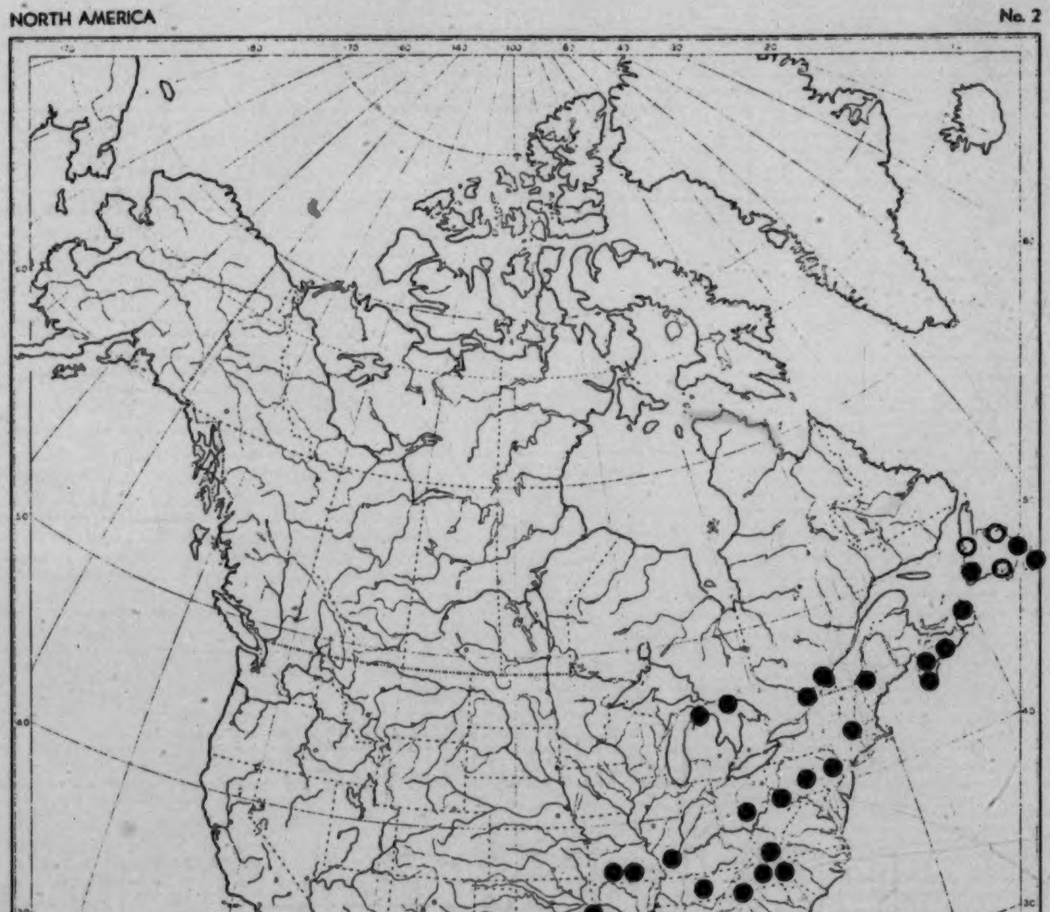
Cecalyphum spurium (Hedw.) P.-Beauv., Prodr. 51. 1805.

Plants medium to large, up to 8.0 cm tall, in tufts or loose mats, dark-green, usually growing on sandy soil. Stems moderately tomentose, tomentum brown. Leaves diverging from stem at a wide-spreading angle, (2) 4.0-7.5 (9) mm long, base ovate, concave, widest point at or slightly below middle, gradually acuminate to an acute apex, when dry twisted to falcate-secund, when moist erect and imbricate, slightly falcate-secund, lamina undulate; margins unistratose, serrate in upper 1/3; costa narrow, 90-120 (130) µm wide just above alar region, subpercurrent to slightly excurrent, toothed on abaxial surface in upper 1/3, papillose in upper half, rarely smooth, in median transverse-section showing 6 to 8 guide cells and 2 stereid bands, the adaxial band strong and extending well into apex, the adaxial band weaker and sometimes ending in upper 1/3, abaxial external layer of cells usually differentiated from stereids by large lumens, adaxial external layer not differentiated; alar cells brown, bistratose, thin-walled, not extending to costa; basal cells just above alar region (40) 60-90 (100) µm long, thick-walled, pitted, with an abrupt change to median cells about 1/3 from base; median cells short, 8-14 (20) µm, triangular to quadrate and irregular, thick-walled; cells of upper 1/3 very irregular, triangular, quadrate or rectangular, usually wider than long, 5.0-10 (16) µm in greatest dimension, thick-walled; cells of margin sometimes forming a weak border with cell ends comprising serrations. Perichaetial leaves usually shorter than stem leaves, innermost ones abruptly narrowing to a subulate tip.

Dioicous, male plants dwarfed and growing on tomentum of female. Monosetous, setae yellow, (2.0) 3.0-4.0 cm long. Capsules curved, usually bent at a sharp angle at junction with seta, 1.5-2.5 mm long, lightly ribbed, slightly strumose, neck very short; exothecial cells thick-walled, rectangular to quadrate, triangular in neck; stomates few in one row at base of capsule; opercula rostrate, 2.0-2.5 mm long; annulus of 2 to 3 rows of large, thick-walled, hyaline cells, often remaining attached to operculum; peristome teeth dark-red, vertically striate, about 0.5 mm long, 70-90 (105) µm wide at base, divided half way into 3 or rarely 2 segments. Spores green to brown, papillose, (18) 20-23 µm. Chromosome number, n=12 (11+x+y).

Habitat and Distribution (Fig. 50): *Dicranum spurium*, like *D. condensatum*, grows on sandy soil, although usually not on pure sand as is often the case with the latter species. It also occurs more frequently in forest habitats and is probably more shade tolerent than *D. condensatum*. It is almost circumboreal in distribution with its range in North America extending from Newfoundland southward into

FIGURE 50. The North American distribution of *Dicranum spurium* Hedw.


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO

North Carolina and westward into Michigan, Missouri, and Arkansas. It does not extend as far south as its close relative, *D. condensatum*, nor does it extend far onto the coastal plain of the south-eastern United States. The species is reported from Europe including Scandinavia, Germany, Hungary, Poland, Romania, and Russia. In Asia it is found in Siberia and Japan.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 95 (NY, US, CANM). Drummond, Musci Amer. (Rocky Mtns.) 90 (NY, FH, CANM). Drummond, Musci Amer. (Southern) 47 (DUKE). Holzinger Musci Acroc. Bor. Amer. 228 (NY), 228b (MIN, NY, CANM, DUKE). Macoun, Can. Musci 96 (CANM, US, DUKE, NY).

CANADA. *Nova Scotia*: Anapolis Co., Kejimkujik National Park, *Ireland 12419* (ALTA). Shelburn Co., 6.4 km S of upper Ohio, *Ireland 12296* (ALTA). Halifax Co., Shubencadie, Grand Lake, *Prince 6003* (MICH). *Ontario*: Great Cloche Island, Manitoulin Dist., *Cain 1935* (DUKE). *Newfoundland*: St. George's Dist., 6 km NNE of Coalbrook, *Hancock* and *Butler 883* (ALTA). Trinity North Dist., 4 km N of Trinity Bay, *Brassard 7117* (ALTA).

U.S.A. Arkansas: Polk Co., Camp Bard, S of Mena, *Anderson 11437* (DUKE). *Illinois*: Pope Co., Lusk Creek Canyon, *Sharp 6323* (TENN). *Maine*: Norway, *Bacon* May 19, 1929 (COLO). *Michigan*: Emmet Co., Wycamp Lake, *Steere 3032* (MIN). *Missouri*: Reynolds Co., Mill Creek, 3.2 km E of Iron Co. line, *Redfearn 13725* (TENN). Texas Co.

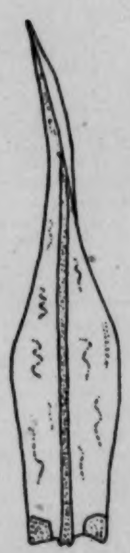
SW 1/4 Sec. 35, T28N, R7W, Redfearn 14021 (TENN). North Carolina: Alexander Co., near Kiddenite, Anderson 7595 (DUKE). Burk Co., Linville Gorge, Anderson 20292 (DUKE). Macon Co., 4.8 km NE of Highlands, Anderson 10041 (DUKE). Orange Co., Duke Forest, Peterson May 8, 1975 (ALTA). Ohio: Hocking Co., Welch 17209 (MIN). Pennsylvania: Huntingdon Co., Wiley July 20, 1939 (DUKE). Monroe Co., Buskell, Bartram 1939 (DUKE). Virginia: near Marion, Britton May 23, 1892 (NY).

Dicranum spurium is one of the most distinctive members of the genus and one of the easiest in North America to recognize. The broad, erect-spreading leaves with imbricate tips make the species unmistakable in its typical form; however, in some of the smaller forms it might be confused with *D. condensatum* as they both grow in sandy habitats and have capsules that are attached to the seta at a sharp angle (Fig. 51-11). In such cases it is necessary to examine the areolation in the upper portion of the lamina. *Dicranum spurium* has a number of cells in this area that are wider than long (Fig. 51-6) while *D. condensatum* rarely has cells that are wider than long.

Nomenclature: In Hedwig's original description (1801), there are three specimens listed (syntypes), one collected by Timm,

FIGURE 51. *Dicranum spurium* Hedw.

1-4	Stem leaves (14x)
5	Perichaetial leaf (14x)
6	Upper laminal cells (280x)
7	Median laminal cells at the margin (280x)
8	Median laminal cells (280x)
9	Basal laminal cells (280x)
10, 11	Capsules (10x)
12	Peristome tooth (140x)
13	Median transverse-section (140x)



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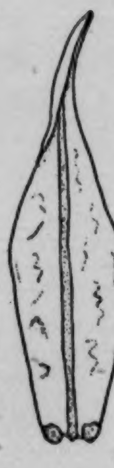

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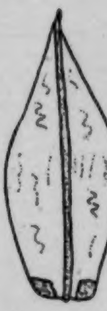

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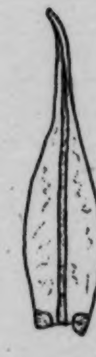

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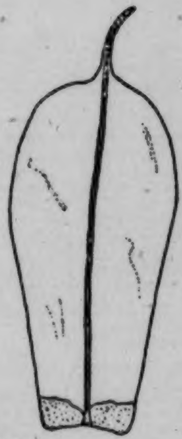

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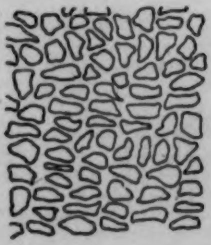

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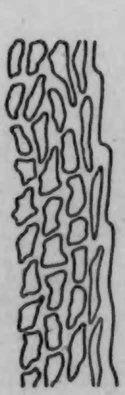

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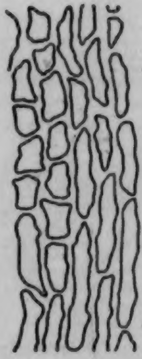

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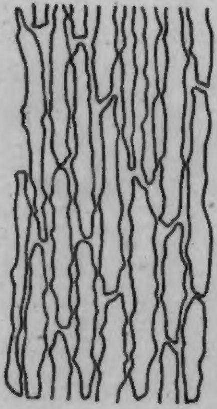

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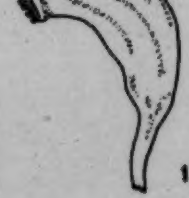

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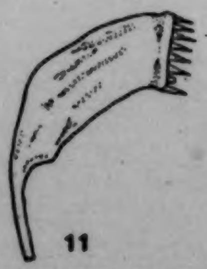

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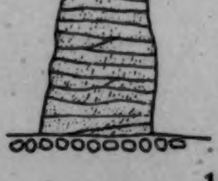

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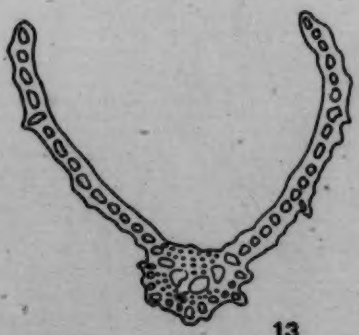


13

one by Bridel, and one from Erlangen (Germany). There are no specimens in Hedwig's herbarium that bear either the name of Timm or Bridel; however, there is one that has "Erlang 1796" written on the label. This specimen is probably one of the syntypes referred to in the protologue and was one of those used by Hedwig to base his concept. In addition, there is one other specimen of interest in Hedwig's herbarium. This specimen does not bear a collector's name nor does it have a locality on the label, but it does have "Hedw. St. cr. II. p. 82 t. 30" which is also quoted in the original description. This specimen is the only one mounted on paper identical to other Hedwig types (ex. *D. condensatum*), and it is possible that this specimen might have been the major specimen from which Hedwig's work was done. Unfortunatley, I cannot determine this, and as a result, I do not wish to select a lectotype at this time. Both specimens are excellent specimens of *D. spurium* and either would make a good lectotype.

17. *Dicranum acutifolium* (Lindb. and Arn.) C. Jens. *in* Weim. Foert. Skand. Vaext. Moss. 2: 18. 1937.

Dicranum bergeri var. *acutifolium* Lindb. and Arn., K. Svensk. Vet. Akad. Handl. 23 (10): 79. 1890.

Types: "... Jenisei ... 63-70^{o}n ... Mai (Surget) mit jungen Fruchtstielen, am Juli (N. Tunguska) mit jungen, bedeckelten Früchten, am 22 Juli (Plachino) und 30 Juli (Dudinka) mit alten Früchten ...". Syntypes - Yenisei, Plachino, 67^{o}40'N, July 22, 1876, col. Arnell (H!).

Dicranum bergeri subsp. *rupincola* Kindb., Eur. and N. Amer. Bryin. 2: 193. 1897.

Type: "Canada, Rocky Moutnains, Hector, rocks, Aug. 13, 1890. Macoun" (Lectotype-S!; Isotype-CANM!)

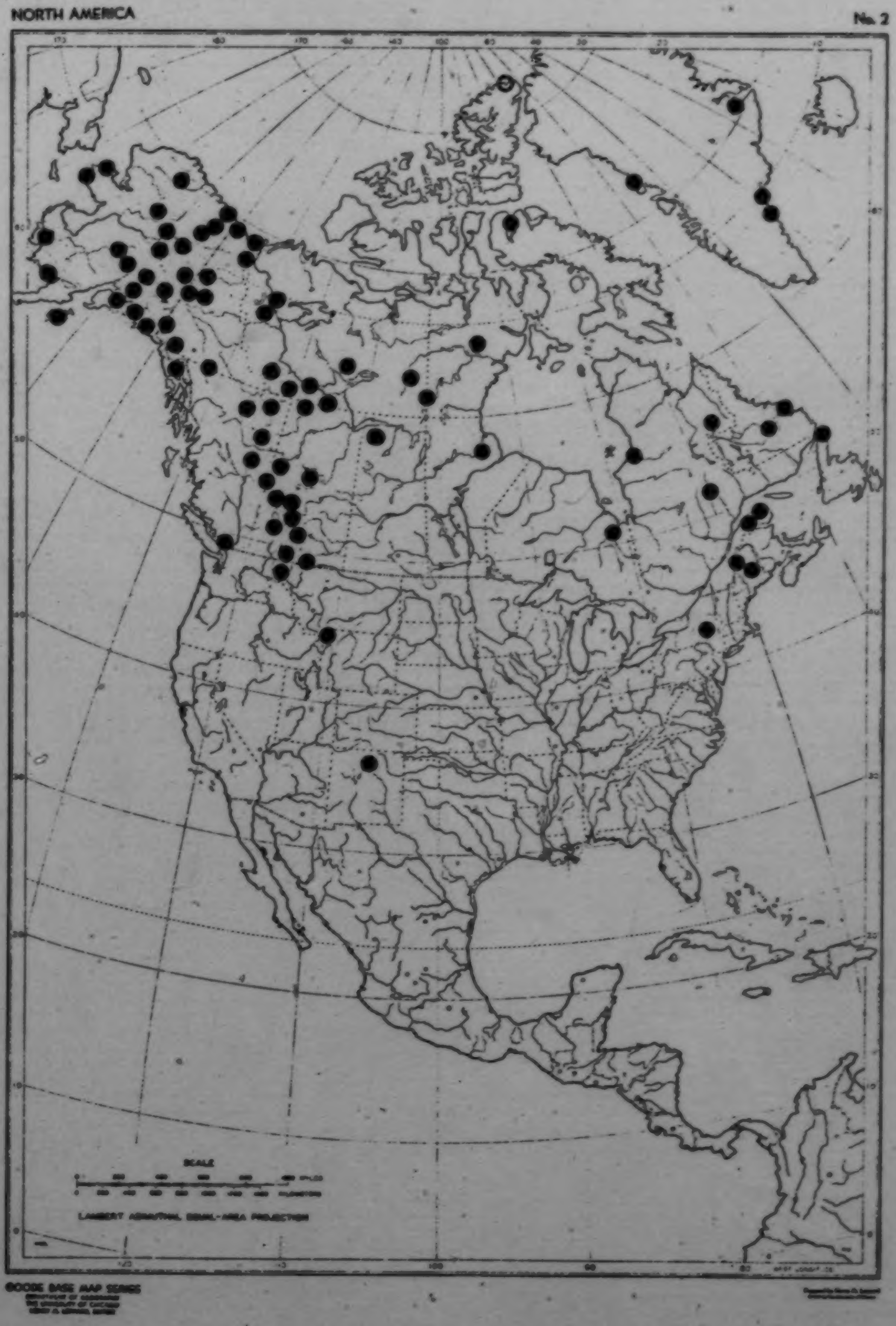
Dicranum rupincola (Kindb.) Perss., Bryologist 57: 196. 1954.

Plants small to medium, up to 5.5 cm tall, in compact tufts in exposed areas or as single stems among other bryophytes in well sheltered areas, light-green, growing on soil or humus. Stems lightly tomentose, tomentum light- to dark-brown. Leaves when dry falcate-secund to twisted, when moist erect and loosely imbricate, slightly undulate, lanceolate, (2.5) 3.0-6.5 (7.5) mm long, gradually tapering to an acute apex, strongly keeled in upper half; margins unistratose, occsioanally bistratose in spots, serrate in upper 1/4; costa narrow (70) 89-95 (105) µm wide just above alar region, percurrent or slightly excurrent, slightly toothed on abaxial side of apex, papillose to smooth farther down, in median transverse-section showing 4 to 6 guide cells and 2 well developed stereid bands, the abaxial band much larger than the adaxial, both extending well into the apex, abaxial layer of external cells slightly differentiated by large lumens, adaxial layer not differentiated; alar cells brown, thin-walled, occasionally slightly thick-walled, bistratose, often extending to the costa; basal cells just above alar region (30) 65-89 (95) µm long, thick-walled, slightly pitted or rarely smooth, with a gradual change to short rectangular, quadrate or triangular median cells, (8) 12-25 (35) µm long, thick-walled, pitted or smooth, upper cells subquadrate or triangular, rounded, thick-walled, not pitted, 8-20 µm long, marginal cells similar to median cells. Perchaetial leaves shorter than stem leaves, sharply narrowing into a smooth or slightly papillose, subulate tip.

Dioicous, male plants minute and growing on the tomentum and leaves of female plants. Monosetous, setae light-brown to light-red, (1.5) 2.0-2.5 cm long. Capsules curved, 1.2-2.5 mm long, slightly ribbed, usually strumose, neck distinct and slightly elongate; exothecial cells short-rectangular, thick-walled; stomates few, in one row at base of capsule; opercula rostrate, 1.5-2.2 mm long; annulus of 2 to 3 rows of large, thick-walled, hyaline cells annulus usually fragmenting; peristome teeth yellow to red, about 0.5 mm long, vertically striate, 65-90 µm wide at base, divided half way down, often more, into 2 segments. Spores green to brown, (10) 14-17 (23) µm. Chromosome number unknown.

Habitat and Distribution (Fig. 52): This species is frequently found in the moss carpets of higher latitude, montane-boreal forests and tundra habitats. It seems to prefer mildly calcareous substrates as evidenced by mires and fens that are usually present in general area where specimens are collected. It often occurs in the forest areas

FIGURE 52. The North American distribution of *Dicranum acutifolium* (Lindb. and Arn.) C. Jens.


NORTH AMERICA
No. 2
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES

surrounding these mires and bogs and, as a result, might be taken for its relative *D. undulatum*.

It is distributed across the Arctic and boreal region of North America ranging from Alaska to Ellesmere Island and also extends along the western cordillera south to New Mexico, and as far as the Adirondack Mountains of New York in the east. It is quite common in Alaska andalong the Canadian Rocky Mountains and is less frequent in the arctic regions of eastern Canada. It is probably widespread in this area, but at present, the region has not been sufficiently collected to substantiate the distribution.

Selected Specimens Examined: EXSICCATI. Grout, N. Amer. Musci Perf. 259 as *D. fuscescens* (DUKE, FH). Macoun, Can. Mosses, Series 1908, 33 as *D. bergeri* v. *rupincola* (FH, MICH), 53 as *D. subulifolium* .

CANADA. Alberta: McKenzie Hw., Mile 269, 59°28'N, 117°11'W, LaRoi July 17, 1971 (ALTA). Grand Cache area, 5.8 km S of Two Lakes, Peterson 1236 (ALTA). Swan Hills, 2.4 Km N. of Goose Mt., Vitt 11729 (ALTA). Wilmore Wilderness Park, along Wildhay River, Peterson 3423 (ALTA). Jasper Nat. Park, Mt. Edith Cavell, Peterson 3523 (ALTA). Waterton Nat. Park, Upper end of Belly R. trail, Kuchar B5134b (ALTA). British Columbia: Fort Nelson area, 160 km W of Fort Nelson, Peterson 2975 (ALTA). Prince George area, Pine Pass at Azouzetta Lake, Peterson 3154 (ALTA). Newfoundland: Cook Harbor, White Bay, 51°31'N, 55°53'W, Tuomikoski 3476 (HSC). Northwest Territories: Chick

Lake, 65°50'N, 128°10'W, Gubbe 6 (ALTA). Mackenzie River, 65°12'N, 127°07'W, Brodie 101 (ALTA). Glacial Lake basin 20.8 km WNW of Norman Wells, Reid 385 (ALTA). Mile 62 of Yellowknife Hwy., 61°03'N, 117°22'W, LaRoi July 15, 1961 (ALTA). Yukon Territory: Swift River 59°51'N, 121°41'W, LaRoi Aug. 1, 1961 (ALTA). Marshall Creek, 60°50'N, 137°20'W, LaRoi Aug. 4, 1961 (ALTA). Kluane Lake area, 61°57'N, 140°32'W, Vitt 6131 (ALTA). Dawson area, 64°05'N, 139°33'W, Vitt 7867 (ALTA). Mt. Klotz, 65°22'N, 140°06'W, Vitt 7563 (ALTA).

U.S.A. Alaska: Gryaling Lake, 67°57'N, 143°10'W, Sikoryak 78 (ALTA). Pillar Mt., Kodiak Island, Bishop June 14, 1972 (ALTA). Index Mt., 69°15'N, 144°10'W, Sikoryak 94 (ALTA). Carlo Creek, 63°33'N, 148°49'W, LaRoi Aug. 13, 1961 (ALTA). Maine: Oxford Co., Richards 6017 (DUKE). Piscataquis Co., Thoreau Spring, Hermann 19287 (DUKE). Montana: Lake McDonald, Williams 195 (F). New York: Watson Hallow, Wiley Sept. 3, 1938 (DUKE). Wyoming: Lower Geyser Basin, Williams 1444 (F).

Dicranum acutifolium is one of the least understood species in North America. It is a distinct species, that is often mistaken for either *D. undulatum* or *D. muehlenbeckii* and at times may be confused with *D. fuscescens* or *D. elongatum*. This is understandable since it may, at times, morphologically intergrade with each. The critical characters in determining *D. acutifolium* are the areolation in the upper portion of the leaf, the shape of the leaf apex, and the capsule shape. The leaf apex is narrowly actue (Fig. 53-5), but not as long

FIGURE 53. *Dicranum acutifolium* (Lindb. and Arn.) C. Jens

1-4 Stem leaves (14x)

5 Stem leaf apices (14x)

6 Perichaetial leaf (14x)

7 Upper laminal cells (280x)

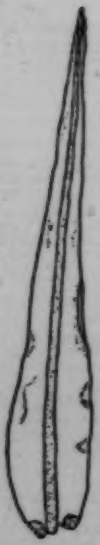
8 Median laminal cells (280x)

9 Basal laminal cells (290x)

10, 11 Capsules (10x)

12 Peristome tooth (140x)

13 Median transverse-section (140x)



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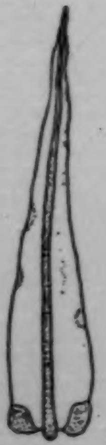

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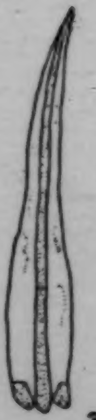

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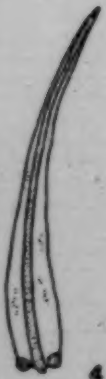

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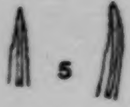

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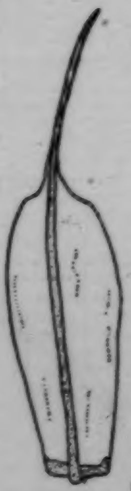

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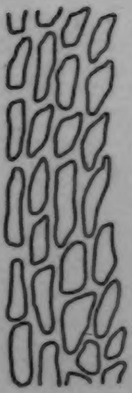

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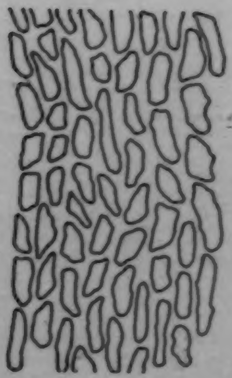

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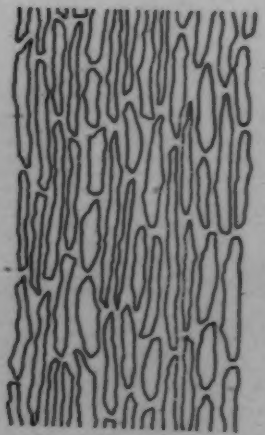

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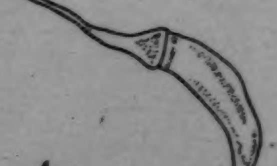

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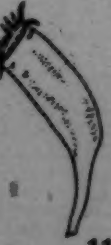

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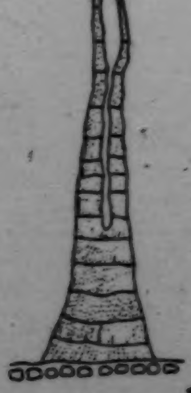

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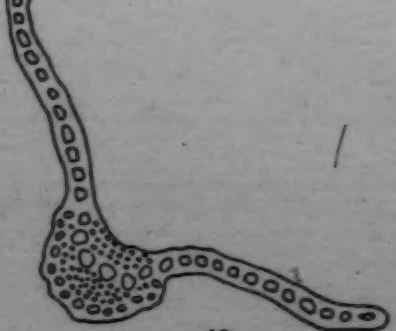


13

as that of *D. fuscescens*; the costa is percurrent or slightly excurrent, which is also different from the blunt apex and subpercurrent costa of *D. undulatum*. Rarely, *D. undulatum* will have a narrow apex and in such cases it can usually be distinguished from *D. acutifolium* by its habitat of fens and mires. *Dicranum acutifolium* may grow in the forest surrounding the area, but usually not in the fen or mire as such. The areolation of the upper lamina is the most important character in separating *D. acutifolium* from *D. fuscescens* and *D. elongatum* since it has many triangular and variously angled and pitted cells (Fig. 53-8) while those of *D. fuscescens* and *D. elongatum* have fairly regular, quadrate or short-retangular cells with no pits (Fig. 27-7). The capsule of *D. acutifolium* (Fig. 53-10) has a longer neck than that of *D. fuscescens* (Fig. 27-10) and the leaves are keeled, which differs from the tubulose condition of *D. muehlenbeckii*.

Nomenclature: Specimens I have placed under this species have been referred to by the name of *D. sendtneri*, which is a name first used by Limpricht in 1890, forty-seven years before the combination *D. acutifolium* (Lindb. and Arn.) C. Jens. was used. Lindberg and Arnell (1890) described *D. acutifolium* as a variety of *D. bergeri* in the same year that Limpricht described *D. sendtneri*. According to Jensen (1939) and Persson (1954) Limpricht's name should be rejected because it is impossible to determine what he was referring to. Limpricht based his description on specimens, collected by O. Sendtner in the

Sudetic Mountains, which were named *D. elongatum* by the collector. Apparently these collections are inseparable mixtures of *D. elongatum* and *D. majus* (Persson, 1954) and the name *D. sendtneri* Limpr. should be considered ambiguous.

18. *Dicranum ontariense* Peterson, Canad. J. Bot. 55: 988. 1977.

Type: *"In sylvis umbrosis Canadae superioris vulgare"* Drummond, Musci Am. (Rocky Mt.) I No. 86, 1828 as *Dicranum undulatum* var. *foliis angustioribus, subtortuousis*. (Holotype-NY!) (Isotypes -FH! NY! DUKE!)

Dicranum drummondii Sull. Mosses U.S., 23. 1856. *non D. drummondii* C.Müll. Syn. Musc. Frond. 1: 356. 1848.

Type: "Lake Superior, Agassiz., Oakes., Sull. and Lesq., Musci Bor. Am. (ed. I) 69b: (Lectotype-NY!) (Isotypes-NY!, DUKE!)

Dicranum drummondii C. Müller forma *minor* C. Müll., Syn. Musc. Frond. 1: 356. 1848.

Dicranum drummondii C.Müll. subsp. *drummondii sensu* Mizush., Journ. Jap. Bot. 45: 158. 1970.

Dicranum wilsonii Sull. *ex* Peterson, Canad. J. Bot. 55: 988. 1977.(pro. synon.)

Plants in loose mats, up to 8.0 cm tall, dark-green to light-green, growing on forest floor, or rarely on wood. Stems densely tomentose, tomentum brown to white, extending to apex. Leaves when dry twisted or falcate-secund, when moist falcate-secund, slightly undulate, (4) 6-8 (10) mm long, long lanceolate, gradually tapering to a sharply acute apex; keeled in the upper half, papillose on abaxial surface; margins strongly serrate in the upper 1/3, serrations often of whole cells, unistratose or bistratose in spots; costa narrow (90) 110-130 (145) μm just above alar region, slightly excurrent or percurrent, strongly toothed on upper abaxial side, teeth often forming ridges 1/2 way down leaf, in median transverse-section showing 7 to 9 guide cells and 2 well developed stereid bands, both extending well into the apex, abaxial layer of external cells well differentiated from stereids by large lumens and often projecting as teeth on surface, adaxial layer not differentiated; alar cells brown, bistratose, thin-walled, not extending to costa; basal cells just above alar region elongate, up to 90 μm long, pitted or smooth, thick-walled, with an abrupt change to shorter median cells about 1/3 from base; median cells short rectangular to quadrate, in uniform rows, thick-walled, (8) 12-18 (24) μm long, cells of tip similar, sometimes triangular, marginal cells usually elongated, up to 65 μm long, forming a weak border. Perichaetial leaves shorter than stem leaves, innermost ones abruptly narrowed to a subulate tip.

Dioicous, male plants dwarfed and growing attached to tomentum of female. Polysetous, setae yellow to light-brown, (1) 2-5 per perichaetium, 2-3 cm long. Capsules yellow to brown, 2-3 mm long, slightly curved, nodding, ribbed, neck short; exothecial cells rectangular, irregularly angled, thick-walled. Opercula rostrate, 1.5-2.5 mm long; annulus fragmenting, of 2 rows of enlarged, clear cells; peristome teeth dark-red, vertically striate, ±0.5 mm long, 80-90 (110) µm wide at base, divided half way down into 2 or 3 segments. Spores papillose, (8) 14-19 (22) µm. Chromosome number unknown.

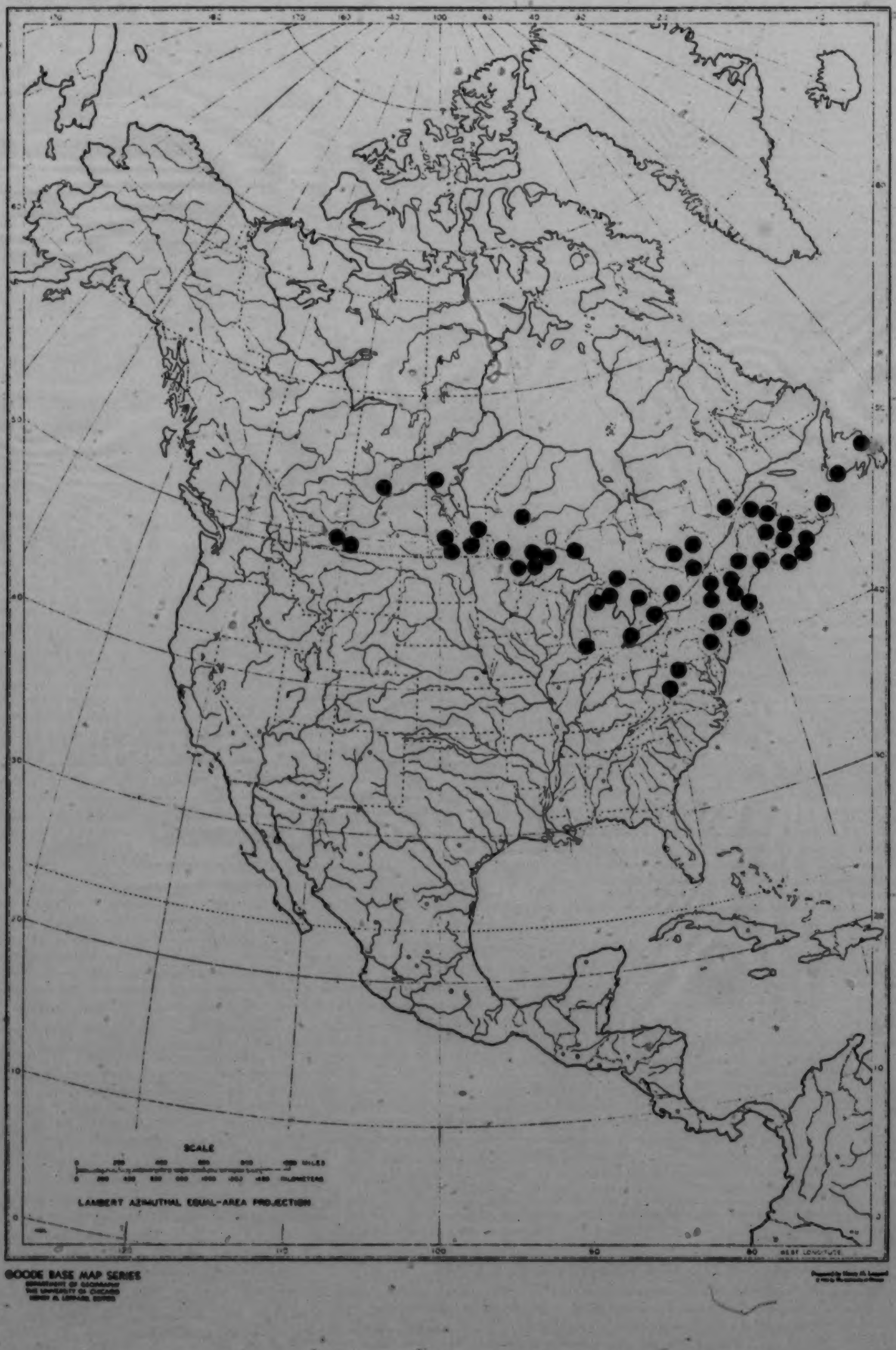
Habitat and Distribution (Fig. 54): This species is endemic to North America and is restricted to a rather narrow band extending north and south of the Canada-United States border from Newfoundland southward to West Virginia, and westward through the Great Lakes region into the Cypress Hills of Alberta. Its typical habitat is that of soil or humus in fairly densely shaded forests. It rarely occurs on logs or stumps. The species has been reported from Kentucky and North Carolina, but all specimens I have seen from these areas are *D. condensatum* Hedw. Steere *et al.* (1977) reported *D. ontariense* from the Nahanni region of the Northwest Territories. All specimens I have examined from this area that might be taken for *D. ontariense* are *D. acutifolium* (Lindb. and Arn.) C. Jens. In my opinion, *D. ontariense* does not occur in the northwest.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. Supp. I. 474 (NY, US, CANM). Drummond, Musci Amer. (Rocky Mts.) 86 as *D. undulatum* var. (NY, FH, DUKE). Grout, N. Amer. Musci Perf. 374 (Basin Falls, Buckfield, Maine) (MIN, UTAH, CANM). Holzinger, Musci acroc. Bor. Amer. 130 in part, 131, 432 (CANM, NY, FH). Macoun, Can. Musci 47 (CANM, NY). Macoun, Can. Mosses 1908 series 43 (CANM, FH).

FIGURE 54. The known distribution of *Dicranum ontariense* Peterson

NORTH AMERICA

No. 2


SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Sull. and Lesq., Musci Bor. Amer. (ed. I) 68b (DUKE, NY). (ed. II) 88 (DUKE). All except Drummond's #86 are cited as *D. drummondii*.

CANADA. Alberta: Cypress Hills, 5.1 km SW of Elkwater, Bird 4500 (UAC). Manitoba: 2.8 km W of Stockton, Bird 8541 (UAC). Reed Lake, 54°35'N, 100°17'W, LaRoi June 24, 1961 (ALTA). Long Lake, 50°52'N, 95°23'W, LaRoi June 15, 1961 (ALTA). Riding Mt. Nat. Park, Rowe 2 (CANM). New Brunswick: Glouster Co., 47°28'N, 65°00'W, Ireland 14287 (ALTA). Kent Co., 46°38'N, 64°57'W, Ireland 14167 (ALTA). Restigouche Co., 47°53'N, 66°08'W, Ireland 14389 (ALTA). Newfoundland: Rencontre West, 47°38'N, 56°40'W, Tuomikoski 1075 (CANM). 12.4 km S of Terra Nova, Damman 5711 (CANM). Nova Scotia: Anapolis Co., Kejimkujik National Park, Ireland 12458 (ALTA). Ontario: Pellee Pt. Macoun 57 (DUKE). Heron Bay, Schofield 42923 (DUKE). Blue Lake Prov. Park, Vitt 4490 (ALTA). Quebec: Baie Comeau, 49°18'N, 68°05'W, LaRoi Aug. 1, 1962 (ALTA). Gatineau Park, NE of Luskville, Peterson 2390 (ALTA). Saskatchewan: Prince Albert Nat. Park, 53°57'N, 106°29'W, LaRoi June 8, 1961 (ALTA). Cypress Hills, Lonepine campsite, Bird 4658 (ALTA).

U.S.A. Indiana: Tremont, Dunes St. Park, Flowers 4218 (COLO). Michigan: Cheboygan Co., Gates Bog area, Vitt 3531 (ALTA). Minnesota: Tilson Bay, Rainy Lake, Moore 11873 (MIN). New York: Essex Co., Chilson Lake, Harris 1899 (DUKE). Bluff Head, Lake George, Levy 1434 (DUKE). Ulster Co., Fulf Rd., Catskill Mts., Beals Nov. 21, 1927

(DUKE). Greenport, Long Island, Latham 13 (DUKE). New Hampshire: Coos Co., Shelburne, Farlow (DUKE). Plymouth, Grout Sept. 1898 (DUKE). West Virgina: Pocahontas Co., Droop Mt., Gray M1476 (DUKE). Greenbank, Gray M1035 (DUKE).

Dicranum ontariense is a rather large and easily distinguished moss in its typical form due to its polysetous condition, its falcate-secund leaves with twisted tips, and its dense tomentum. Most confusion involves the Eurasian species - *D. drummondii* C.M.. Mizushima (1970), working in Japan, considered these two taxa to be subspecies of *D. drummondii* C.M. using as criteria, " 1) Stems densely radicose, scarcely branched, 2) Leaves oblong lanceolate, long acuminate, 3) leaf cells quadrate or short-rectangular, irregularly arranged and mammillose in the upper part, irregularly fusiform in the middle, and oblong in the lower part, 4) costa spinosely serrate on the back in the upper part.". In addition, she cited the common conditions of tranversely undulate leaves and fascicled setae. All of these states, except fascicled setae are found (in varying degrees) throughout the *Dicranum* section *Spuria* which includes the species *D. spurium* Hedw., *D. undulatum* Brid., *D. acutifolium* (Lindb. and Arn.) C. Jens., *D. condensatum* Hedw., *D. drummondii* C.M., and *D. ontariense*. I find these character states to be useful at the section level, but it is impossible to use them as unifying criteria at the species level. Mizushima separated her subspecies according to 1) size, 2) leaf sheen, 3) leaf length to width ratio, 4) difference in thickening of cell walls, and 5) the distribution of spines on the adaxial surface. I consider all except (4) to be valid. The North American material has median cell walls that are irregularly thickened, Mizushima describes them as "regularly thickened", but not to the degree of the Eurasian material. Nevertheless, these differences are sufficient to warrant specific recognition for each taxa, and with the additional peristome and distribution differences, there should be no doubt. Table 8 lists the differences in detail.

Dicranum ontariense can be distinguished from related North American species primarily by its fascicled setae which usually occur in groups of three to five per perichaetium; however, as many specimens are collected in the sterile state, gametophytic characters must be relied upon for identification. It is most often confused with *D. undulatum* Brid., a widespread species usually found in mire habitats and associated with *Sphagnum* spp. Typically, *D. undulatum* has 1) rounded to broadly acute apices with the costae ending 3 to 12 cells below the tip, 2) slightly serrated margins with cells about the same size as the more median ones, 3) few papillae, usually near the tip on the adaxial side of the costae, and 4) a very gradual transition from the short median cells to the long cells. In contrast, *D. ontariense* has 1) long acuminate tips with slightly excurrent costae (Figs. 55-2), 2) strongly serrated margins with occasional long cells at the border (Fig. 55-6), 3) numerous papillae extending down the costa and on the upper laminal surfaces (Fig. 55-12, 55-13), and 4) a rather

FIGURE 55.

55-1. *Dicranum drummondii* C.M. (not treated)

55-2 through 55-13 *Dicranum ontariense* Peterson

1-4	Stem leaves (14x)
5	Perichaetial leaf
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (140x)
12	Median transverse-section (70x)
13	Upper transverse-section (140x)

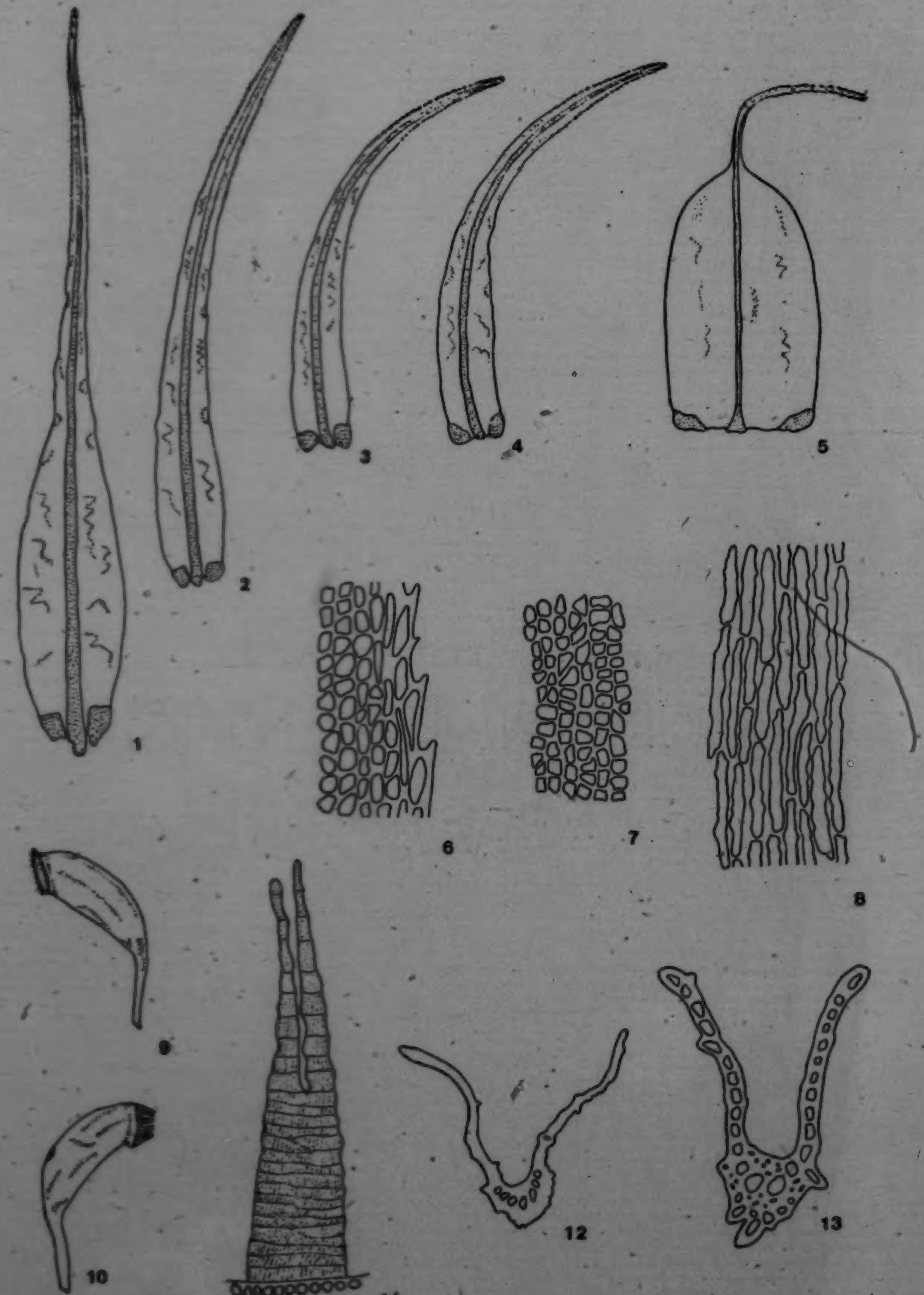


TABLE 8. Major character states differing between *D. ontariense* Peterson and *D. drummondii* C. Müll.

D. ontariense	*D. drummondii*
1. Plants about 2.5-4.0 cm tall and 0.8-1.5 cm wide (Fig. 9-4)	1. Plants about 5.0-8.0 cm tall and 1.0-2.5 cm wide (Fig. 8-4)
2. Leaf length to width ratio about 7.0-10.0 : 1 (Fig. 55-4)	2. Leaf length to width ratio about 6.0-6.7 : 1 (Fig. 55-1)
3. Peristome teeth split into two regular segments (Fig. 55-11)	3. Peristome teeth usually split into three or sometimes two irregular segments
4. Leaves dull	4. Leaves shining
5. Papillae often in the lower half of the leaf.	5. Papillae only in upper half of the leaf
6. Endemic to North America	6. Distributed throughout Eurasia and Japan

abrupt change from short median cells (Fig. 55-7) to the longer basal cells (Fig. 55-8). *Dicranum spurium* and *D. condensatum*, two species generally found south of the distribution of *D. ontariense*, can be distinguished by short, wider than long, median cells which usually extend to near the leaf base. These species usually occur on sandy soils while *D. ontariense* grows on humus in lush forests. The only other species occurring in the range of *D. ontariense* that might cause confusion is *D. fuscescens* Turn. It is a somewhat smaller species, usually found on decaying wood, and can be distinguished microscopically by median cells that are rectangular to squarish, and arranged in uniform rows, while *D. ontariense* has median cells that are often irregularly angled and not arranged in uniform rows (Figs. 55-6, 55-7).

Nomenclature: The nomenclatural history of this species dates to 1847 when W.P. Schimper (*in* Bruch *et al.*, 1836-1855) described *D. robustum* from specimens collected in Norway by Blytt and Schimper, the lectotype of which is located in Schimper's herbarium (BM-K) (Isoviita, 1977). In addition, Schimper cited No. 86 of Drummond's Musci Americani (Rocky Mts.), which is labelled *Dicranum undulatum* var. *foliis angustioribus subtortuosis*. He did indicate the latter specimen was different than the Norwegian specimens by calling it "forma minor". In 1848, Müller realized that the name *D. robustum* Blytt *ex* Schimp. was a later homonym of *D. robustum* Hook. (a southern hemisphere species that is now included in the segregate genus

Dicranoloma) and redescribed the northern hemisphere species as *D. drummondii*, using the name of the North American collector. Upon close examination of both descriptions, it is evident that the authors were describing only the Norwegian specimens. Schimper states *"e basi late lanceolata"* and his plate 36 of Bryologia Europaea represents only the Norwegian specimens. Müller says *"e basa lata robusta..."* and *"dentes persist. subirregulariter bifidi."*. Again, he refers only to the Norwegian specimens.

Lindberg (1865) recognized the problem that the 1828 Drummond specimen was, in fact, different from the Norwegian material and was worthy of specific rank. He renamed the Eurasian species *D. elatum* and left the name *D. drummondii* attached to the North American species citing Sullivant (1856) as the author (for mentioning it in his *Mosses of the U.S.*). As a result, the name *D. elatum* has been extensively used in Europe, but the older name *D. drummondii* C.M., not *D. drummondii* Sull., has been commonly applied to the North American material. Mizishima (1970), working in Japan, accepted this nomenclature and reduced the two taxa to *D. drummondii* subsp. *drummondii* (North American) and *D. drummondii* subsp. *elatum* (Eurasian).

There is an unpublished letter in the Farlow Herbarium (FH) written by Sullivant in 1868 disavowing any credit for discovery of *D. drummondii* and stating that Lindberg's views are "... not tenable ... Müller should not be deprived of his species solely for a false synonym ..." I agree with Sullivant that the name *D. drummondii* is still valid and should be placed with the Eurasian species typified by the Norwegian specimens. Therefore, *D. elatum* is a synomym *D. drummondii* C.M. and the North American species typified by Drummond's No. 86, is without a name. Sullivant also recognized this problem and proposed the name *D. wilsonii* in honour of the British bryologist who suggested that Drummond's No. 86 might be a new species; however, he never published the name.

It is unfortunate that a Eurasian species must be referred to as *D. drummondii* since Drummond was not associated with the species and did most of his collecting in North America. In 1977 (Peterson 1977b) I decided it was not worth compounding this problem by naming a North American endemic after a European bryologist (i.e. Wilson) who did not work in the area. I proposed the name *D. ontariense* as a *"nomen novum"* since the Ontario area is essentially the geographic center of the species distribution (Fig. 54). Unfortunately, I neglected to specify exactly what name *D. ontariense* was replacing. As a result, Isoviita (1977) discussed the problem anew and concluded that my name of *D. ontariense* is valid as I quoted the latin phrase *"foliis angustioribus subtortuosis"* which qualifies as a latin diagnosis; therefore, it should be concidered a *"species novum"* instead of a *"nomen novum"*.

19. *Dicranum undulatum* Brid. Jour. f. Bot. 1800. 1(2): 294. 1801.

Types: *"Dicranum undulatum a scopario, momente Schradero, distinctissimum. Tolle etiam Weberi synonymon ... Inter synonyma adde ... Dicranum polycarpon Röhlingii ..."* (Types not seen).

Dicranum bergeri Bland. *in* Sturm, Deutschl. Fl. 2(10): 7. 1809.

Type: Musci Frond. Exs. 114. 1805. (Isotype-FH!).

Dicranum rugosum Kindb., Ottawa Natural. 4: 61. 1890.

Type: "In damp woods near Halifax, Nova Scotia (June 21st, 1883). J. Macoun, Coll." (Lectotype-S!).

Dicranum schraderi Web. et Mohr., Bot. Tasch. 177. 1807. *Nom. illeg. incl. spec. prior.*

Cecalyphum undulatum (Brid.) P.-Beauv., Prodr. 52. 1805. *Nom. illeg. incl. gen. et. spec. prior.*

Plants in dense to loose mats, up to 14 cm tall, often forming compact mats up to 60 cm across on *Sphagnum* hummocks, light-green to dark-green. Stems sparsely tomentose, tomentum light- to dark-brown. Leaves when dry slightly twisted or falcate-secund, when moist erect and imbricate, strongly undualte, occasionally papillose on abaxial laminal surface, (4.0) 6.0-8.5 (11) mm long, lanceolate, gradually narrowed to an acute to broadly acute or blunt apex, strongly keeled in upper 1/2 to 1/3; margins unistratose, entire in lower 2/3, serrulate to serrate in upper 1/3, often coursely serrate at apex; costa narrow, 95 (110-120) 130 µm wide just above alar region, subpercurrent or rarely percurrent, toothed to smooth on abaxial surface, costa in median transverse-section showing 5 to 7 guide cells and 2 well developed stereid bands, both bands extending well into apex, the abaxial layer of external cells slightly differentiated from stereids by large lumens, the adaxial layer not differentiated; alar cells hyaline to brown, bistratose, thin-walled, not reaching costa; basal cells just above alar region (30) 45-75 (90) µm long, thick-walled, pitted, rarely thin-walled and smooth, with a gradual change to short rectangular, thick-walled median cells, (7.0) 14-20 (30) µm, not in uniform rows; upper cells subquadrate or triangular, sometimes wider than long, (4.0) 6.0-8.0 (14) µm long; marginal cells similar to median cells. Perichaetial leaves shorter than stem leaves, innermost ones abruptly truncate or sinuately truncate with a short subulate tip.

Diocous, male plants dwarfed, growing on tomentum of female plants. Monosetous, setae yellow to brown, 1.5-3.5 (4.5) cm long, slightly ribbed, not strumose, neck short but distinct; exothecial cells short-rectangular to quadrate, thick-walled; stomates few, in one row at base of capsule; opercula rostrate, 1.5-2.5 mm long; annulus fragmenting, of 2 or rarely 3 rows of large, thick-walled, hyaline cells; peristome teeth yellow to red, vertically striate, about 0.5 mm long, (55) 70-85 (100) µm wide at base, divided more than half way down into 2 or 3 segments. Spores green to brown, papillose, (16) 20-26 µm. Chromosome number, n=12.

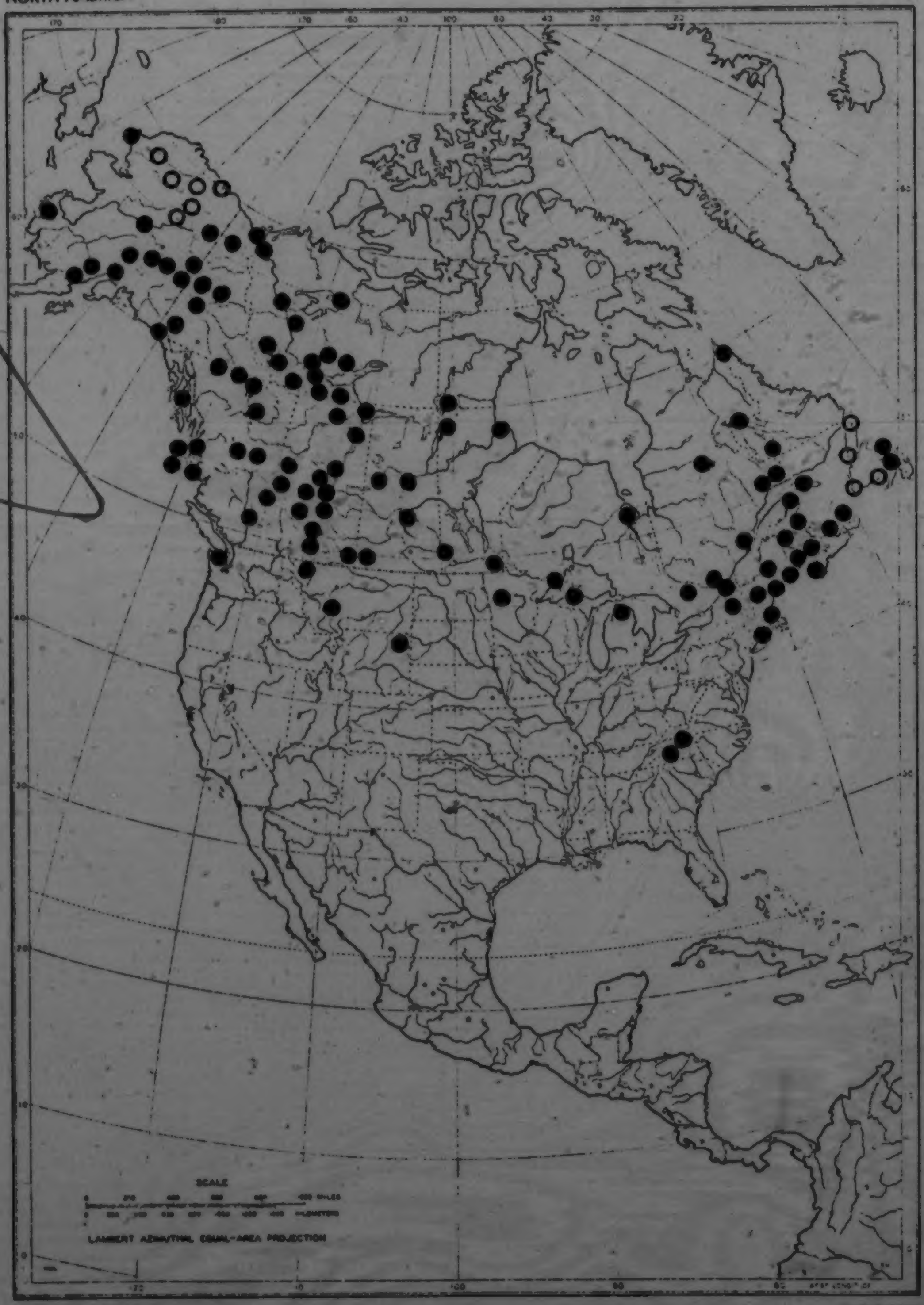
Habitat and Distribution (Fig. 56): *Dicranum undulatum* is typically a mire species, often growing on raised areas or hummocks in *Picea mariana* wetlands . It rarely grows on soil or wood in open areas. In Alberta, it is common is calcareous fens throughout the boreal and mountain regions. It is often associated with other byrophytes, noted for their tendency to grow in calcareous fens, among which are *Auldcomnium palustre*, *Meesia uliginosa*, *Tomenthypnum nitens*, *Catoscopium nigritum*, and *Camplyium stellatum*. It is not common in the Arctic of North America and I have not seen any specimens from north of the Arctic Circle except for northern Alaska, Inuvik in the Northwest Territories, and Great Bear Lake (which is on the Arctic circle). This species is very common in the boreal forest, south of this region and may be dependent upon the more protected habit for survival. The total distribution of *D. undulatum*, in North America, ranges from the west coast of Alaska across Canada to the east coast of Newfoundland, and south as far as the Olympic Peninsula in Washington, and the Bighorn National Forest in Wyoming in the west, and in the east as far south as the mountains of North Carolina. Elsewhere in the world, it is reported from Scandinavia, Bohemia, the Alps, eastern Russia, Siberia, and Japan.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 93 as *D. schraderi*, 94 as *D. schraderi* var. (NY, FH, CANM, US). Blandow, Musci Frond. 114 as *D. bergeri* (FH). Drummond, Musci Amer. 87, 88 as *D. schraderi* (NY, FH, CANM, MICH). Holzinger, Musci Acroc. Bor.

FIGURE 56. The North American distribution of *Dicranum undulatum* Brid.

NORTH AMERICA

No. 2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Amer. 130 in part (NY, FH, CANM). Macoun, Can. Musci 32, 45 as *D. schraderi* (US, TENN, CANM, NY). Renauld and Cardot, Musci Amer. Sept. 12 as *D. bergeri* (FH, CANM). Sull., Musci Allegh. 163 as *D. schraderi* (NY, FH, MICH, US). Sull. and Lesq., Musci Bor. Amer. (ed. I) 67 as *D. schraderi* (DUKE, FH, NY). Sull. and Lesq., Musci Bor. Amer. (ed. II) 84 as *D. schraderi* (FH, MICH).

CANADA. Alberta. Pigeon Lake, Turner 9904 (ALTA). Wylie Lake, Canadian Shield, Vitt 5066 (ALTA). Swan Hills, 16 km E of Goose Mt., Vitt 4023 (ALTA). Willmore Wilderness Park, along Wildhay River, Peterson 3449 (ALTA). Edmonton area, Heatherdown bog 56°36'N, 114°09'W, Peterson 943 (ALTA). Rocky Mt. House, 48 km S of town, Peterson 3301 (ALTA). Kananskis, 4.8 km S of lakes, Peterson 3221 (ALTA). Cypress Hills, 8 km SW of Elkwater, Bird 4576 (CANM). British Columbia: Prince George aarea, 28 km N of Summit Lake, Peterson 3183 (ALTA). Liard Hot Springs, 59°25'N, 126°08'W, Peterson 2954 (ALTA). Manitoba: Whiskey Jack Lake, 58°25'N, 101°55'W, Scotter 3530 (ALTA). Riding Mt. Nat. Park, Rowe 12 (MICH). Newfoundland: Avalon Peninsula, Conception Bay, Fernald and Weigand 6520 (MIN). Bonavista North Dist. 5 km N of Middle Brook, Brassard 7055 (ALTA). New Brunswick: Albert Co., Fundy Nat. Park, Ireland 11583 (ALTA). Charlotte Co., 16.8 km S of Dumbarton, Ireland 13166 (ALTA). Nova Scotia: Inverness Co., Cape Briton Highlands Nat. Park., Ireland 11832 (ALTA). Shelburne Co., Upper Clyde River, Ireland 12354 (ALTA). Ontario: Algonquin

Park, Macoun, Canadian Mosses 32, June 13, 1900 (FH, MICH). Prince Edward Island: Kings Co., 46°28'N, 62°13'W, Ireland 14106 (ALTA). Quebec: Gatineau Park, NE of Luskville, Peterson 2382 (ALTA). St. Urbain Co., Kucyniak *et al.* 45-47 (MICH). Anticosti Island, Macoun, Canadian Mosses 32, Aug. 12, 1883 (MICH). Saskatchewan: Gem Lakes 3.5 km E of Beaver Creek, Anderson 1188 (ALTA). Cypress Hills, Lonepine campsite, Bird 4460 (CANM). Northwest Territories: Horn Plateau, NE of Fort Simpson, Rowe July 7, 1961 (ALTA). Heart Lake, Vitt 4940 (ALTA). Inuvik, 69°29'N, 133°38'W, Friesen and Hettinger Sept. 28, 1973 (ALTA). Norman Wells, Jasieniuk 2275 (ALTA). Yellowknife, Ingraham Trail, Jasieniuk 2286 (ALTA). Great Bear Lake, Port Radium, Kucyniak 48-85 (MICH). Yukon: Summit Lake, 67°42'N, 137°28'W, Packer and Lemay 34 (ALTA). Clinton Creek area, W of Dawson, 64°17'N, 140°27'W, Vitt 10765 (ALTA).

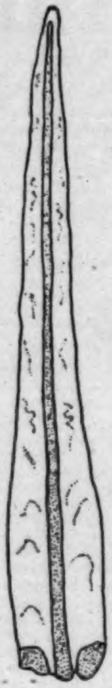
U.S.A. Alaska: Pillar Bay, Rigg Aug. 11, 1929 (WTU). Alaska Hwy., mile 1318, Lutz 50-184 (WTU). Newhalen, near Newhalen River, Thomas Sept. 30, 1951 (WTU). Fairbanks Quad. 65°10'N, 147°15'W, Calmes 637 (ALA). Kasigluk, 61°10'N, 162°10'W, Thomas 12-54 (ALA). Connecticut: Vernon Centre, Lorenz Jan. 30, 1906 (MIN). Maine: Piscataquis Co., 17.6 km NE of Schoodi Lake, Hermann 19656 (CANM). Massachusetts: Amesbury, Huntington May 14, 1904 (US). Michigan: Cheboygan Co., Mud Lake, Crum July 11, 1948 (CANM). Minnesota: Ithasca State Park, 12.1 km along Wilderness Drive, Horton 1150 (ALTA). Montana: Columbia Falls, Williams, Montana Mosses 195 (MIN). Lost Fork Creek, Little Belt Mts., Leiberg 783 (F), New Hampshire: Mt.

Washington, Bliss 1959 (ALTA). New York: Essex Co., Algonquin Peak, Ketchledge 692 (MICH). North Carolina: Mt. Pisgah, Anderson 20628 (DUKE). Bluff Mts., Anderson 19947 (DUKE). Washington: Port Angeles, Harthill Mar. 26, 1959 (DUKE). Wisconsin: Bayfield Co., Lake Superior, Squaw Pt., Flowers 9889 (COLO). Wyoming: Bighorn National Forest, Weber *et al.* B4664 (COLO).

Dicranum undulatum is one of the easiest members of the genus to recognize, since it typically grows in mire habitats, has leaves that are plainly undulate and, when moist, they are erect and somewhat imbricate. Also, it produces a single seta per perichaetium. In most circumstances, these macroscopic states are all that is necessary to identify it. In rare instances it may intergrade morphologically with either *D. ontariense* or *D. acutifolium*. In such cases it usually occurs just outside its typical mire habitat and the specimens may be more slender and contorted than normal. In these situations it may be distinguished microscopically from *D. ontariense* by median cells that are slightly longer (Fig. 57-8), about 20 µm long, as compared to about 12 µm (Fig. 55-7) in *D. ontariense*. Also, *D. undulatum* never has the longer cells along the margin which maybe found in *D. ontariense* (Fig. 55-6) nor are the marginal serrations as strong. From *D. acutifolium*, *D. undulatum* can be distinguished by more broadly acute leaf apices (Fig. 57-5), a generally subpercurrent costa (Fig. 57-2), and upper cells that are about 10 µm or less in length (Fig.57-7). *Dicranum acutifolium*

FIGURE 57. *Dicranum undulatum* Brid.

1-4	Stem leaves (14x)
5	Stem leaves apices (14x)
6	Perichaetial leaf (14x)
7	Upper laminal cells (280x)
8	Median laminal cells (280x)
9	Basal laminal cells (280x)
10, 11	Capsules (10x)
12	Peristome tooth (140x)
13	Median transverse-section (140x)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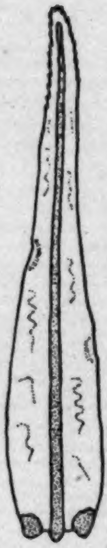
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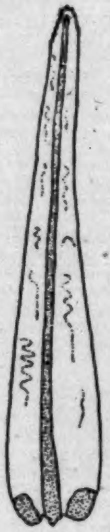
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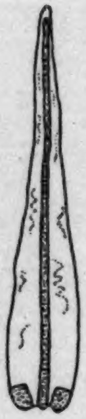
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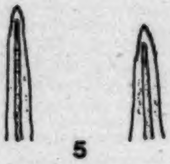
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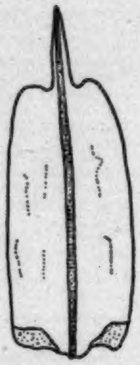
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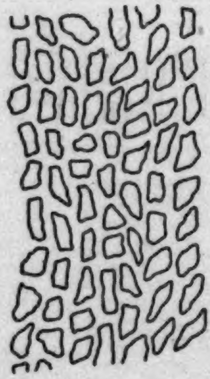
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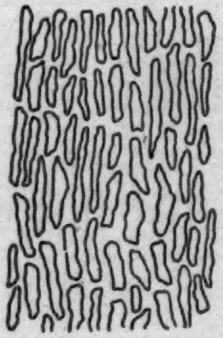
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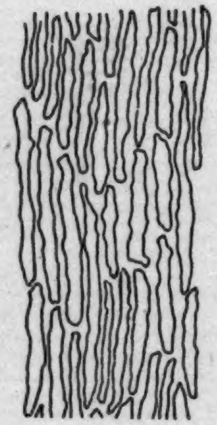
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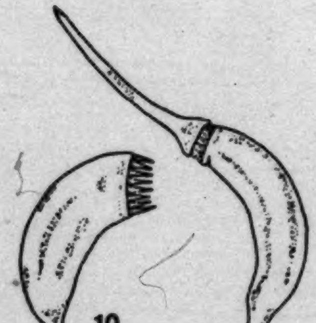
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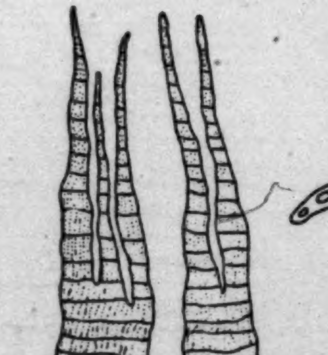
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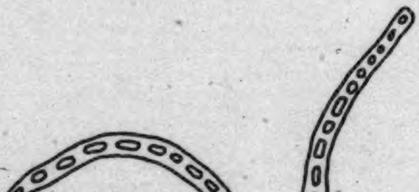
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has a narrowly acute apex (Fig. 53-5), a percurrent to slightly excurrent costa (Fig. 53-3), and upper cells that are about 20 µm in length (Fig. 53-7).

Nomenclature: The original diagnosis of *D. undulatum* was published in *Journal fur die Botanik 1800* which was circulated in 1801 at the Leipzig Easter Fair on April 19 of that year (Sayre, 1959). This is the date that was determined by the 1910 Botanical Congress to represent the starting date for bryological nomenclature because Hedwig's *Species Muscorum* was also circulated at the 1801 Easter Fair.

With April 19, 1801 as the nomenclatural starting date, Bridel's name is valid; however, it was generally overlooked and the name *D. bergeri* Blandow, published in 1809, has been extensively used for this species. The situation was further complicated when the 1950 Botanical Congress at Stockholm changed the nomenclatural starting date to December 31, 1801, thus nomenclaturally eliminating Bridel's name. At that time, Blandow's name was the valid one. However, this was not to last, as the 1959 Botanical Congress at Montreal again changed the nomenclatural starting date in order to include several important publications in the year 1801, and established the new starting point as January 1, 1801. As a result, Bridel's name is valid.

I have examined Bridel's herbarium and found one specimen named *D. undulatum* by Bridel; however, it is not one of the specimens listed in the description. According to Isoviita (*pers. comm.*) the type is not in Bridel's herbarium and this one specimen may in fact be a syntype of Blandow's *D. bergeri* since it is annotated by Blandow and a reference is made to Blandow's exsiccati set of 1805. Since the type is not in Bridel's herbarium I choose not to designate a lectotype at this time.

Section: *Dicranum* Hedw. Spec. Musc. 126. 1801.

Lectotype: *Dicranum scoparium* Hedw.

Plants up to 15 cm tall. Leaves sometimes undulate, falcate-secund to straight and spreading, lanceolate to ovate-lanceolate; apex acute, obtuse or rarely cucullate; upper cells elongate and usually pitted; median transverse-section of costa showing one or two rows of guide cells and 2 stereid bands, lumens of stereids small (<1/2 the wall thickness), 2 to 4 lamellae often present on abaxial costal surface. Capsules curved, ribbed; neck short, annulus absent (except in *D. angustum*).

20. *Dicranum angustum* Lindb. Medd. Soc. F. Fl. Fenn. 6: 252. 1881

Types: "... Norbotten samt på åtskilliga ställen i finska Lappmarken af hrr Norrlin och Hult ..." (Lectotype - Norbotten, Hult, July 3, 1877-H-SOL!) (Syntypes - Norbotten, Hult, June 27, 1877-H-SOL!; Lapmarken, Hult, July 13, 1877-H-SOL!; Hult, Aug. 5, 1887-H-SOL! Norrlin, July 3, 1867-H-SOL!)

Dicranum laevidens Williams, N. Am. Fl. 15(2): 126. 1913.

Tupe: "Klondike River near mouth of Bonanza Creek, 3 miles from Dawson, Yukon, July 3, 1899. R.S. Williams 539." (Holotype-NY!)

Plants in loose cushions, up to 6.5 cm tall, light-green usually growing on humus or soil. Stems slightly tomentose, light- to dark-brown. Leaves when dry erect and somewhat imbricate, when moist erect and spreading, not undulate, 4.0-7.0 (8.5) mm long, lanceolate, narrow at base and tapering to an acute apex, not keeled, smooth on both surfaces; margins unistratose, entire or serrulate near the apex; costa narrow, 80-90 (105) μm wide just above alar region, subpercurrent to percurrent, smooth, costa in median transverse-section showing 5 to 7 guide cells and 2 well developed stereid bands, both extending about 2/3 the length of the costa, neither abaxial or adaxial layer of external cells differentiated from stereid cells; alar cells brown, bistratose, thin-walled, not extending to costa; basal cells just above alar region elongate-rectangular, (40) 60-100 μm long, thick-walled, pitted; median cells elongate, 50-60 (75) μm long, strongly pitted; upper cells elongate, (25) 30-40 μm long, 4.0-7.5 μm wide, slightly pitted. Perichaetial leaves slightly shorter than stem leaves and abruptly narrowing to a subulate tip.

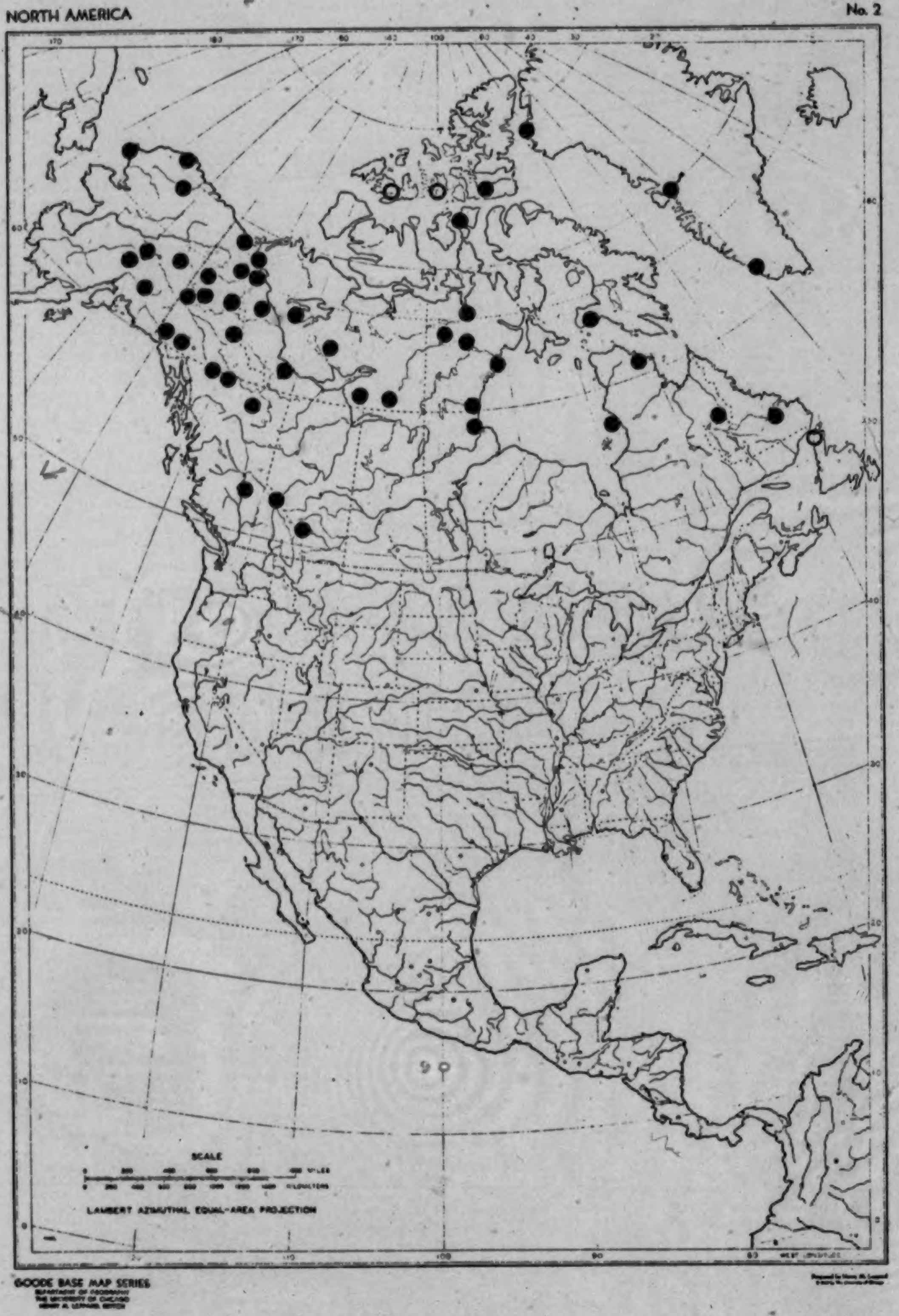
Dioicous, male plants smaller than female, growing intermixed with female plants or as separate cushions. Monosetous, setae light- to dark-brown, 1.8-2.5 cm long. Capsules light-brown, 2.5-3.0 (3.2) mm long, curved, ribbed, not strumose, neck short; exothecial cells short-rectangular, thick-walled, pitted, about 50 μm long; stomates in one row of base of capsule, 30-32 (35) μm long; opercula rostrate, about 1.5 mm long; annulus of 2-3 rows of large, thick-walled, hyaline cells; peristome teeth red, about 0.5 mm long, 70-80 (95) μm wide at base, divided about half way down into 2 segments, vertical striations weak, especially near apex of teeth; spores green to brown, 14-20 μm, papillose. Chromosome number unknown.

Habitat and Distribution (Fig. 58): *Dicranum angustum* is an infrequently reported species, however it is fairly common in moist arctic tundra habitats, especially in exposed areas. It occurs from the west coast of Alaska, across the Canadian Arctic to Devon Island, Baffin Island, and Labrador, and extends southward along the Canadian Rocky Mountains as far as Banff National Park, and, at times, it is quite common in the tundra habitats in the alpine zone. The species is also found in Greenland, and it is reported from Scandinavia, the mountains of eastern Russia, and several areas of Siberia.

Selected Specimens Examined. EXSICCATI. Steere and Holmen, Bryophyta Arctica Exs. 3 (ALTA).

CANADA. *Alberta*: Jasper National Park, Signal Mtn., *Peterson 3654* (ALTA). Moraine Lake, *Flowers 10310* (COLO). *British Columbia*: Bennett City, *Williams 545* (F). Well Gray Provincial Park, Battle Mtn., *Ahti* and *Ahti 14767* (CANM). Summit Lake, 58°38'N, 124°43'W, *Peterson 2964* (ALTA). *Newfoundland*: Labrador, W. Tunnavik, *Nutt* and *Haring 5* (DUKE). *Quebec*: Gerin Mtn., 55°04'N, 67°14'W, *Viereck 706* (DUKE). Wakeham (Marcourt), *Polunin 14766-1* (MICH). *Northwest Territories*: Eastern Great Slave Lake Region, 105°30'W, 60°55'N, *Jasieniuk et al. 1227* (ALTA). Mackenzie

FIGURE 58. The North American distribution of *Dicranum angustum* Lindb.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Mtns., SW of Norman Wells, *Rowe 1903* (ALTA). Baker Lake, *Larsen 9-25* (MICH). Fort Simpson, *Jasieniuk 2224* (ALTA). Kwejinne Lake, 267 km NNW of Yellowknife, *Jasieniuk 2322* (ALTA). Baffin Island, Cape Dorset, *Soper 890* (DUKE). Aklavik, *Lynch 24* (LAF). Devon Island, Truelove Lowland, *Peterson 2562* (ALTA). Chesterfield, *Polunin 2233a-5* (MICH). Somerset Island, Fiona Lake, 73°04'N, 95°03'W, *Pasiuk P124* (ALTA). Baker Lake, 64°19'N, 96°04'W, *Gubbe et al. M92* (ALTA). Mackenzie River Delta, 68°35'N, 129°33'W, *Scotter* (ALTA). *Yukon Territory*: Bell River Area, 67°28'N, 137°12'W, *Pollock* June 18-20, 1972 (ALTA). Bonanza Creek, near Dawson City, *Macoun 53* (US). Lake Lindeman, *Williams 539a* (F). Northern Ogilvie Mtns., Nahoni Range, *Vitt 13368* (ALTA). Southern Ogilvie Mtns., 64°22'N, 137°18'W, *Horton 2759* (ALTA).

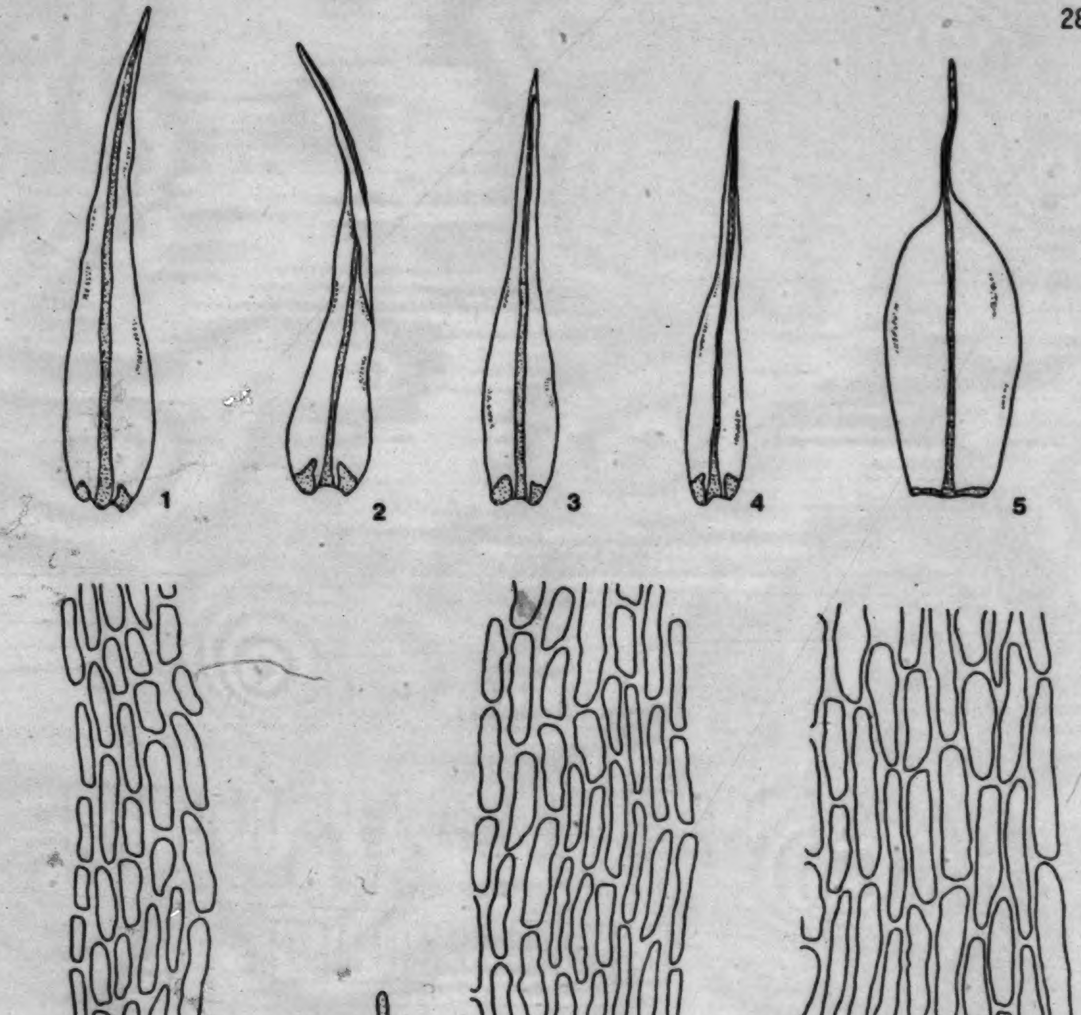
U.S.A. *Alaska*: Barrow, 0.8 km NE of NARL Camp, *Gravesen* Feb. 7, 1971 (ALTA). Umiat, Colville River, *Steere* and *Iwatsuki 74-40* (ALTA). Fairbanks Quadrangle, 16 km W of Ester Dome, *Hermann 20982* (DUKE). Mt. McKenley National Park, 3.2 km N of Camp Denali, *Hermann 21515* (DUKE). Central Yukon River District, *Hermann 21083* (DUKE). Paxton, *Hermann 21183* (US). 69°20'N, 165°10'W, *Bee 520809-51B* (MICH).

Superficially, *D. angustum* appears to be closely related to *D. scoparium*. Indeed, the species is often difficult to separate from the latter, even on close examination. Nevertheless, it is not as closely related to *D. scoparium* as are other less superficially similar species (*D. polysetum* and *D. majus*). For example, *D. angustum* possesses an annulus, while the other members of the Section *Dicranum* do not. This character state, along with smaller capsules (Fig. 59-10) and well developed stereid bands (Fig. 59-12) suggest a possible alliance with *D. groenlandicum* in Section *Elongata* and *D. angustum* may be a species intermediate between these two groups. Because of its long upper cells (Fig. 59-6), curved capsules (Fig. 59-9), and relatively thin leaf cell walls (Fig. 59-7) I am retaining it in Section *Dicranum*.

Sterile material (the usual case) is often difficult to separate from forms of *D. scoparium* and *D. majus* and in such cases it is necessary to examine a costal transverse-section to verify the presence of good stereid bands, and the lack of abaxial lamellae and differentiation of the adaxial costal layer. *Dicranum majus* has at least a few cells in the adaxial layer differentiated by large lumens and may have a double row of guide cells while *D. scoparium* has lamellae or remnants of lamellae (Fig. 68) on the abaxial side of the costa. One other species that might, at times, be confusing is *D. spadiceum*, but its upper cells (Fig. 37-6) are shorter (often <4:1) and it usually has a few differentiated cells in the adaxial layer of the costa (Fig. 37-12).

FIGURE 59. *Dicranum angustum* Lindb.

1-4	Stem leaves (14~~x)~~
5	Perichaetial leaf (4x)
6	Upper laminal cells (280x)
7	Median transverse-section (140x)
8	Basal laminal cells (280x)
9,10	Capsules (10x)
11	Peristome tooth (180x)
12	Median transverse-section (140x)
13	Basal transverse-section



21. *Dicranum polysetum* Swartz, Monthl. Rev. 34. 538. 1801.

Types: Swartz, *Dispositio systematica muscorum frondosorum Sueciae* p. 34 and 87 + III. F.5. 1799. (not seen) *fide* Bridel, 1806.

Dicranum undulatum Ehrh. *ex* Web. et Mohr, Index Musci Pl. Crypt. 2. 1803.

Types: Dillenius, Musc. t. 46. f.16c. and Swartz, *Dispositio systematica muscorum frondosorum Sueciae* t. 3. F.5 (not seen) *fide* Bridel, 1806.

Dicranum rugosum (Hoffm. *ex* Funck) Brid., Musc. Rec. Suppl. 1: 175. 1806.

Bryum rugosum Hoffm. *ex* Funck, Bot. Zeit. Regensberg 2: 69. 1803.

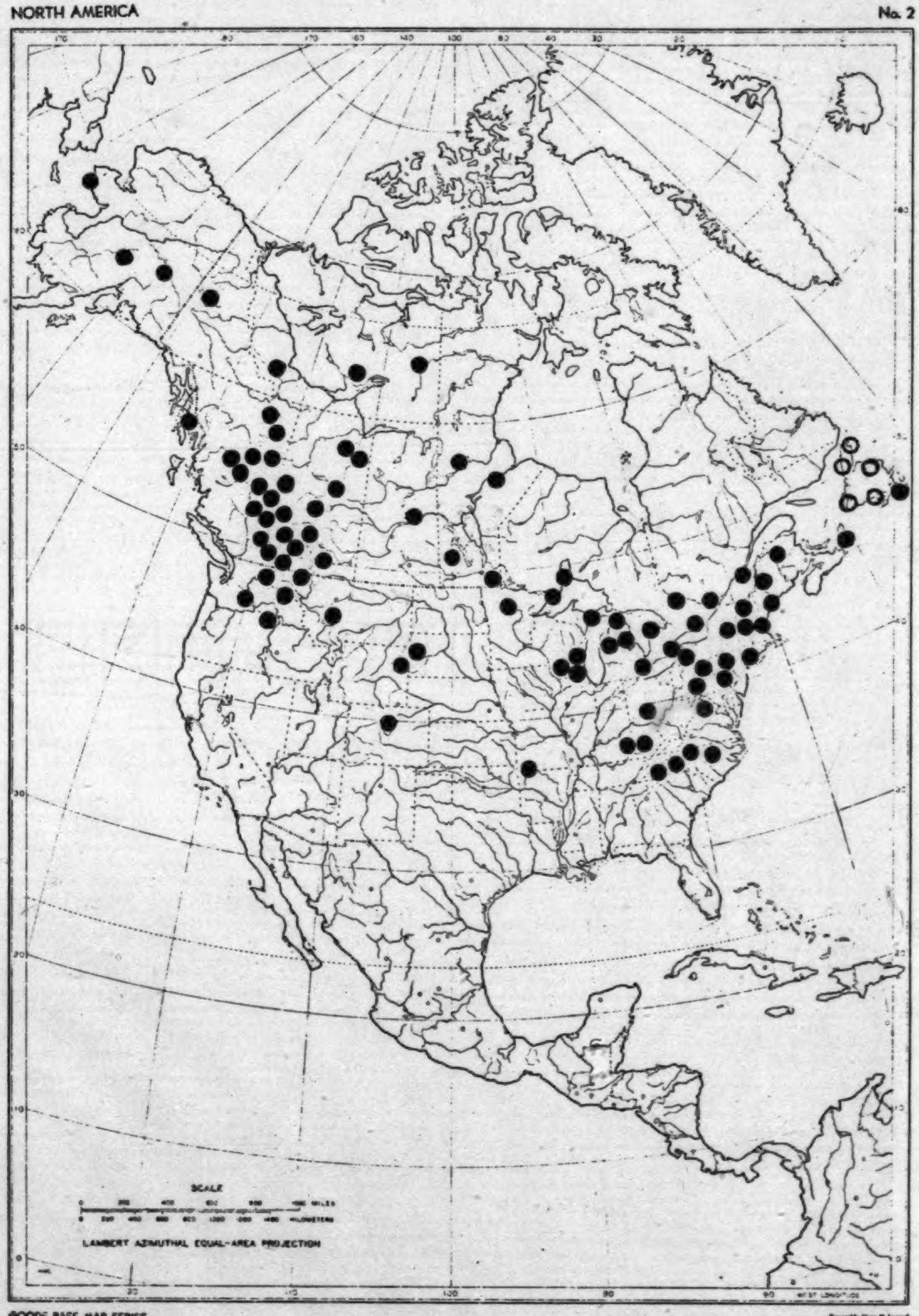
Types: Hoffman, Deut. Fl. II. p. 39. and Dillenius, Musc. p. 357. t. 46. F.16c. (not seen) *fide* Bridel, 1826.

Plants robust, in loose mats, 3 to 12 cm tall, light- green, growing on humus, rarely on soil or decaying wood. Stems densely tomentose, tomentum white to brown. Leaves when dry erect and spreading, similar when moist, strongly undulate to rugose, (7) 10-12 (15) mm long, lanceolate, tapering to an acute apex, not keeled, smooth on both laminal surfaces; margins unistratose, toothed or strongly serrate in upper 1/2; costa narrow, 80-115 µm wide just above alar region, subpercurrent, rarely slightly excurrent, with 2 to 4 unistratose lamellae on the adaxial surface, each lamellae consisting of 1 to 4 cell layers and extending from the leaf tip to 1/2 or 2/3 the length of the leaf; costa in median transverse-section showing 4 to 6 guide cells and 2 well developed stereid bands, the abaxial band often divided into 3 smaller bands by the larger lamellae cells, both bands disappearing in the apex, neither abaxial or adaxial layer of external cells differentiated from stereids; alar cells brown, bistratose, thin-walled not extending to costa; basal cells above alar region elongate, pitted, 40-85 (120) µm long, thick-walled; median cells similar, (50) 80-90 (105) µm long; upper cells similar, 40-70 µm long, 7.0-15 µm wide. Perichaetial leaves slightly shorter than stem leaves, the innermost ones abruptly accuminate to a subulate tip.

Dioicous, male plants dwarfed and growing on tomentum of female plants. Polysetous, usually 3 to 5 setae per perichaetium, 1.8-3.0 (3.5) cm long, yellow to brown. Capsules brown to yellow, 2.0-3.5 mm long, curved, ribbed, not strumose, neck short, exothecial cells rectangular to linear, slightly pitted, thin-walled, about 70 µm long; stomates few in one row at base of capsule, 45-50 (52) µm long; opercula rostrate, curved or straight, 1.5-2.5 mm long; annulus absent; peristome teeth red or red-orange, vertically striate, about 0.5 mm long, 90-110 (130) µm wide at base, divided half way down into 2 or 3 segments; spores papillose, 26-32 µm. Chromosome number, n=11, 12, 12+1.

Habitat and Distribution (Fig. 60): *Dicranum polysetum* is a species that usually grows in well drained habitats in shaded forests. In Alberta it is often found on upper slopes and ridges along with

FIGURE 60. The North American distribution of *Dicranum polysetum* Sw.


NORTH AMERICA
No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 1600 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

feather moss communities that consist of *Pleurozium schreberi*, *Hylocomnium splendens*, and *Ptilium crista-castrensis*. I have also encountered the species in *Picea mariana* bogs, but it then grows near the top of large hummocks that are well drained. The species is circumboreal in distribution, ranging in North America from the east coast of Alaska through the boreal forest eastward to Newfoundland. In the west, it extends southward along the Rocky Mountains as far as Colorado. It is uncommon west of these mountains, having been collected only in central British Columbia, Idaho, Washington, and Oregon. In the east it extends southward, mainly in the deciduous forests, as far as North Carolina and southern Missouri. It is also reported from Bavaria, Spain, western Russia, Siberia, and Japan.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 97 (CANM), 98 (CANM). Drummond, Musci Amer. (Rocky Mtns.) 85 (MICH, CANM). Holzinger, Musci Acroc. Bor. Amer. 134 (MICH, CANM). Holzinger, Musci Acroc. Bor. Amer. *et*. Eur. 589 (MICH, CANM). Macoun, Can. Musci 48 (CANM). Sull. and Lesq., Musci Bor. Amer. (ed. I) 69 (MICH). Sull. and Lesq., Musci Bor. Amer. (ed. II) 87 (MICH). Renauld and Cardot, Musci Amer. Sept. 207 (CANM).

CANADA. Alberta: Banff Springs Golf Course, Crum 3214 (SMS). Cross Lake Provincial Park, Abele 20 (ALTA). Ft. McMurray, about 30 km N of town, Peterson 4477 (ALTA). Cochrane, Nordegg Road, Bird 6233 (LAF). Battle Lake, W of Pigeon Lake, Peterson 1162 (ALTA). Two Lakes, 12.2 km S of campground, Peterson 1201 (ALTA). Kananiskis Dam area, along Whitman Creek, Peterson 2119 (ALTA). British Columbia: Aleza Lake, 1.0 km W of Ranger Station, Peterson 3202 (ALTA). Summit Lake, 124°16'W, 58°41'N, Peterson 3040 (ALTA). Francois Lake, Boas 1073 (DUKE). Frasier River, 4.8 km W of Yellowhead Pass, Crum *et al.* 4840 (DUKE). Malakwa, Krajina 65062267 (DUKE). Manitoba: Menosino, Bird 3302 (LAF). Horseshoe Lake, Scotter 3587 (LAF). Riding Mtn. National Park, Rowe 27 (MICH). New Brunswick: Grand Falls, Habeeb 89 (TENN). Newfoundland: Greene's Harbour, Waghorne, July 9, 1893 (TENN). Nova Scotia: Cape Breton Island, Macoun 719 (DUKE). Ontario: Indian River, N of Owen Sound, Lampton Aug. 5, 1931 (MICH). Thunder Bay Dist., Sibley Peninsula, Garton 2668 (MIN). Ottawa, Rockcliffe, Macoun 117 (DUKE). Quebec: Bellechase Co., S. Camille, Masson 5028 (TENN). Gatineau Park, 45°32'N, 76°00'W, Peterson 2382 (ALTA). Saskatchewan: Candle lake, Swan and Jefferson S-2A (LAF). Northwest Territories: Thelon River, Scotter 4153 (LAF). Yukon: Territory: Dawson City, Bonanza Creek, Macoun Aug. 11, 1902 (CANM).

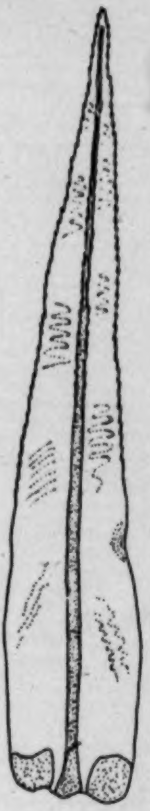
U.S.A. Alaska: Kuskokwim River, 62°40'N, 152°30'W, Viereck 5206 (CANM). Wrangell, Foster 1203 (WTU). Nome, Hansen 49 (COLO). Fairbanks Quadrangle, 64°50'N, 147°25'W, Argus 904 (COLO). Colorado: Boulder Co., Indian Peaks, Reese B-44158. Connecticut: New Haven, Hatcher Nov. 12, 1883 (LAF). Idaho: Bonner Co., Priest Lake, *Peterson* *1112* (ALTA). *Indiana*: Tremont, Dunes State Park, *Flowers* *4218* (COLO). *Kentucky*: Bath Co., Olympia, *Rogers* Oct. 4, 1941 (DUKE). Estill Co., 1.6 km SE of Harg, *Wharton* *419* (CANM). *Maine*: York, Spruce Swamp, *Sanborn* Aug. 1892 (MIN). Gilead, *Seymour*, Sept. 29, 1900 (MICH). *Michigan*: Cheboygan Co., opposite entrance to U.M.B.S., *Snider* *1418* (DUKE). Ostigo Co., *Schnooberger* *2065* (MICH). Montcalm Co., *Schnooberger* *2177* (MICH). Delta Co., *Gleason* *2385* (MICH). Isle Royale, *Langmorthy* *168* (MICH). Iosco Co., NW of Oscoda, *Loughridge* *4241a* (MIN). *Minnesota*: Clearwater Co., 8 km N of Itasca Park, *Buell* *1818* (MIN). Kawastchong Falls, 11.2 km N of Ely, *Holzinger* June 8-10, 1897 (MIN). *Missouri*: Barry Co., 0.8 km E of Roaring River State Park, *Redfearn* *5640* (DUKE). *Montana*: Columbia Falls, *Williams* May 4, 1897 (F). Beet Mtns., *Anderson* *s.n.* (UC). *New Hampshire*: Rockingham Co., Suncook, *Moul* *5659* (MICH). *New York*: Essex Co., Meadow Rd. near Marey Dam, *Norris* *1285910* (TENN). Enfield Gorge, *Kaufman* Nov. 6, 1902 (MICH). *North Carolina*: Franklin Co., Stalling's Crossroads, *Crosby* *2453* (DUKE). Alleghany Co., Stone Mtn., *Anderson* *8209* (DUKE). Durham Co., Aldridge Swamp, *Blomquist* Feb. 25, 1930 (DUKE). *Ohio*: Ross Co., 4.8 km SW of Kingston, *Bartley* *2* (TENN). *Oregon*: Umatilla Co., 46 km W of junction of Hwy. 80N at LaGrade, *Peterson* *1096* (ALTA). *Pennsylvania*: Lancaster Co., Octoraro Creek, *Small* and *Carter* Nov. 23, 1893 (UC). Monroe Co., Hogback Mtn., *Bartram* *185* (MIN). Huntingdon Co., Near Barre

St. P.R.R., Porter, Aug. 1862 (TENN). Vermont: Newfane, Flowers 4380 (COLO). Virginia: Warren Co., Overall Run Falls, Hermann 16394 (DUKE). Washington: Ferry Co., Foster 2331 (WTU). Yakima Co., Silver Springs, Hermann 19099 (WTU). West Virgina: Ridgeville, Harper Aug. 18, 1894 (MICH). Wisconsin: Cederberg, Costello 587 (COLO). Bayfield Co., Raspberry Bay, Flowers 9903 (COLO). Wyoming: Newcastle, Degener and Peiler 17058 (F).

Dicranum polysetum, in its typical form, is the easiest of all Dicrana to recognize. Its spreading, strongly undulate to rugose leaves, multiple setae, and the long cells in the upper lamina (Fig. 61-6) readily distinguish it. No other member of the genus (in North America) has this combination of characters. The only other species with multiple setae are *D. majus* which is never undulate, and *D. ontariense* which has short upper cells (Fig. 55-6). *Dicranum undulatum*, the only other species that might have undulations approaching that found in *D. polysetum*, has short upper cells and single setae. Occasionally, sterile or depauperate specimens may have reduced undulations and may be referred to the ambiguous *D. bonjeanii* De Not. Crum (1973) considered *D. bonjeanii* to be a "pigeon hole" for difficult and morphologically intergrading specimens of *D. polysetum* and *D. scoparium* (see discussion under *D. scoparium*). Specimens of *D. polysetum* that fall into this category can usually be identified by serrations on the upper 1/3 of the margin. Normally specimens of *D. scoparium* that fall into

FIGURE 61. *Dicranum polysetum* Sw.

1-4	Stem leaves (9x)
5	Perichaetial leaf (9x)
6	Upper laminal cells (560x)
7	Median laminal cells (560x)
8	Basal laminal cells (560x)
9, 10	Capsules (10x)
11	Peristome tooth (180x)
12	Upper transverse-section (280x)
13	Median transverse-section (280x)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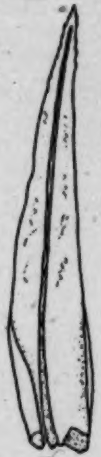
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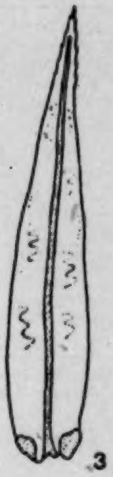
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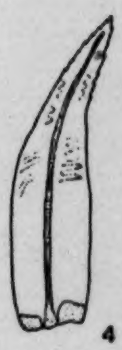
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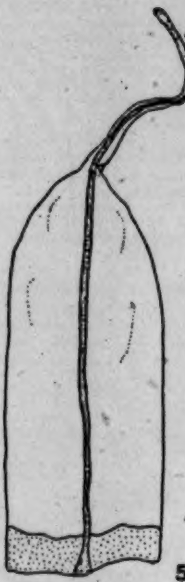
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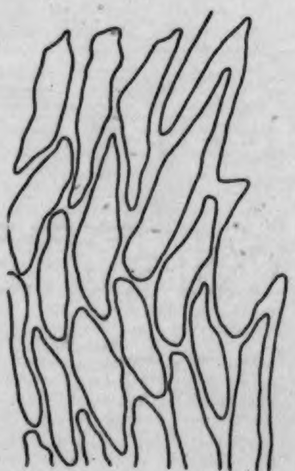
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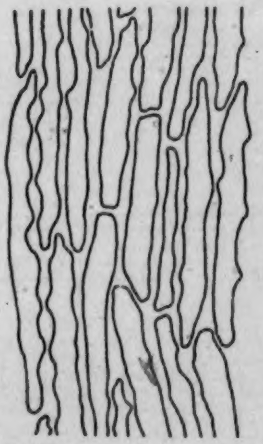
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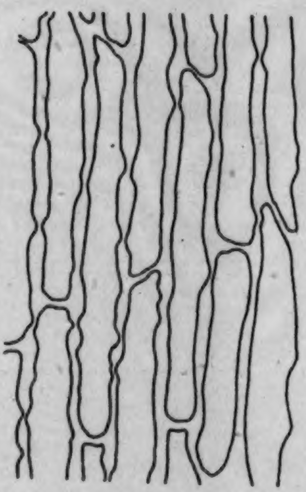
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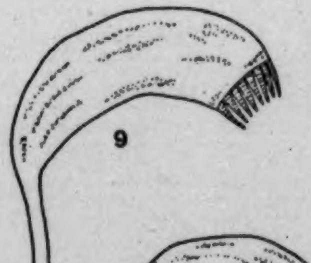
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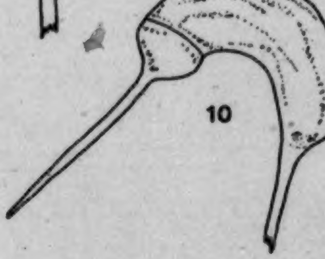
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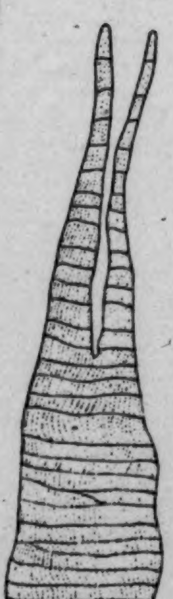
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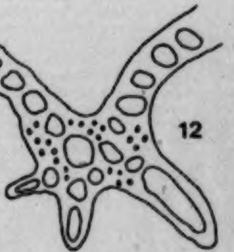
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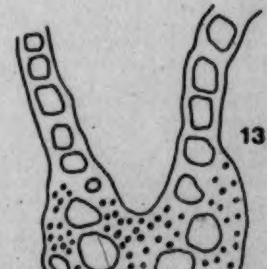

13

this category have entire margins or only a few serrations near the apex.

22. *Dicranum majus* Smith, Fl. Brit. 1202. 1804. *non* Turner, Musci Hib. 58. 1804.

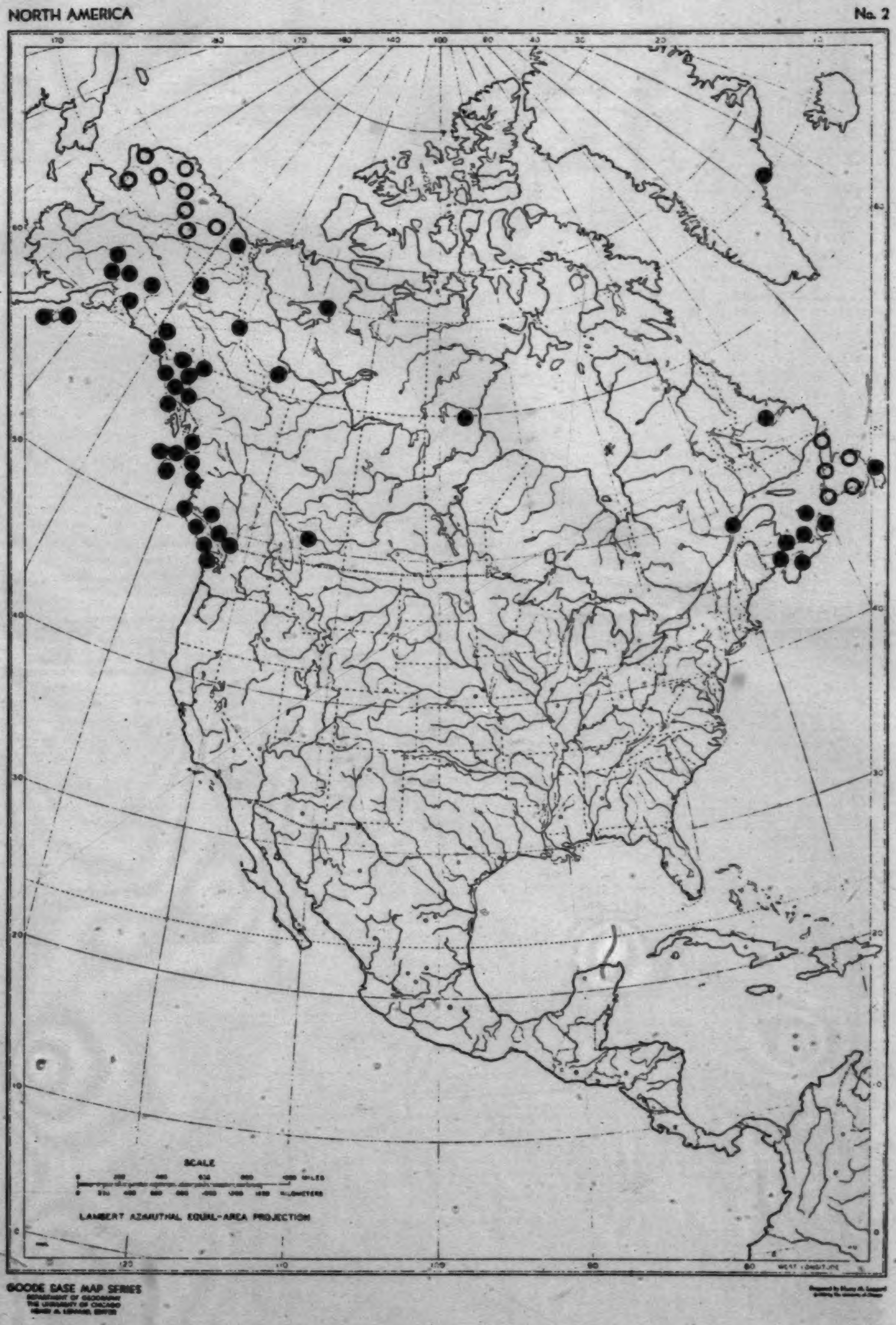
Type: Dillenius, Table 46, Fig. 16.D (specimens unavailable, similar to Figures, Oxford).

Plants in loose mats or tufts, up to 15 cm tall, dark-green, usually with a metallic luster, growing on humus or soil. Stems moderately tomentose, tomentum brown. Leaves when dry falcate-secund or rarely straight, similar when moist, not undulate, (6.0) 8.0-14 µm long, long-lanceolate, tapering to a sharply acute tip, not keeled, smooth on both laminal surfaces, upper lamina occasionally bistratose in spots; margins serrate in upper 1/2 to 1/3, rarely entire, unistratose; costa narrow, 110-125 µm wide just above alar region, subpercurrent to excurrent, no lamellae present; costa in median transverse-section slightly convex and showing 8 to 10 guide cells and 2 stereid bands, guide cells in 2 rows (primary row well defined and continuous with laminal cells, the other more irregular and abaxial to primary row), both stereid bands extending well into apex, abaxial layer of external cells well differentiated from stereid cells by large lumens, adaxial layer occasionally with differentiated cells; alar cells brown to opaque, bistratose, thin-walled, not extending to costa; basal cells above alar region elongate-rectangular, thin-walled, not pitted, 80-100 (120) µm long; median cells elongate-rectangular, slightly pitted, thin-walled, 55-75 µm long; upper cells similar to median, (35) 40-55 µm long, 8.0-20 µm wide. Perichaetial leaves shorter than stem leaves and abruptly narrowed to a subulate tip.

Dioicous, male plants usually dwarfed and growing on tomentum of female plants. Polysetous, usually 3 to 5 setae per perichaetium, setae (2.0) 2.5-3.5 cm long, light-to dark-brown. Capsules brown to light-brown, 2.0-2.5 mm long, curved, ribbed, not strumose, neck short; exothecial cells long-rectangular, thin-walled, pitted, about 100 µm long; opercula rostrate, 1.0-2.5 mm long; annulus absent; peristome teeth red to orange, vertically striate, about 0.6 mm long, 110-130 µm wide at base, divided half way down into 2 or 3 segments; spores brown, finely papillose, 18-24 µm. Chromosome number, n=11, n=12, n=17 (12+5).

Habitat and Distribution (Fig. 62): *Dicranum majus* has an oceanic distribution pattern, ranging in the west from the state of Washington, north along the coast of British Columbia to Alaska and Kodiak Island. In eastern North America it ranges from Nova Scotia and the Gaspé region of Quebec to the middle of Labrador. It also occurs in Japan, the British Isles, and Europe. I have seen one specimen from southern Alberta that has the double row of guide cells of *D. majus*; however, it lacks other diagnostic characters such as the convex costa and the metallic luster found on the coastal specimens.

FIGURE 62. The North American distribution of *Dicranum majus* Sm.


NORTH AMERICA
No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1600 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
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Furthermore, the collection site has been destroyed by a freeway and it has been impossible to collect additional material for study. I have included the specimen in the distribution pattern, but it must be considered tenuous unless additional material is found.

Somewhat reduced forms of this species are occasionally encountered in the arctic or subarctic regions. I have seen specimens from Great Bear Lake, Hudsons Bay, and northern Yukon which seem to retain the characteristic metallic luster found on the more robust coastal specimens, but they usually lack the double row of guide cells. Also, the costa is still somewhat convex (Fig. 63-13) when seen in transverse-section.

Selected Specimens Examined: EXSICCATI. Holzinger, Musci Acroc. Bor. Amer. 278 (CANM, MIN).

CANADA. Alberta: Kananaskis Area, near Seebe, Seaborn 15267 (UAC). British Columbia: Dewdney Island, 52°59'N, 129°40'W, Schofield 41611 (UBC). Morsby Island, Peel Inlet Road, Schofield 15223 (UBC). Vancouver Island, Ucluelet, Schofield 13472 (UBC). S. Graham Island, Trounce Creek, Schofield 15604 (UBC). New Brunswick: Charlotte Co., Grand Manan Island, Gleason 143 (DUKE). Victoria Co., Gold Brook, Schofield 6143 (DUKE). Albert Co., Fundy National Park, Ireland 11302 (ALTA). Newfoundland: Labrador, North West River, Wickes July 29, 1938 (DUKE). Windsor Lake, near St. Johns, Ostafichuk 281-3 (ALTA). Nova Scotia: Halifax, Macoun June 23, 1882 (DUKE). Cape Breton Island, Macoun July 29, 1898 (MIN). Quebec: Saguenay Co., Inlets a Jeremie, Brisson 559 (TENN). Magdalena Islands (France), Bartram 880 (DUKE). Prince Edward Island: Kings Co., 0.8 km N of Glencorradale, Ireland 14078 (ALTA). Queens Co., Strathgartney Park, Ireland 13709 (ALTA). Northwest Territories: Great Bear Lake, Sawmill Bay, Steere 10376 (DUKE). Keewatin Dist., Yathyed Lake, Larsen July 28, 1961 (CANM). Norman Wells, Mt. Hamar, 65°20'N, 126°49'W, Jasieniuk 2308 (ALTA). Yukon Territory: Lake Lindeman, Williams 545 (F). Richardson Mtns., 66°03'N, 135°38'W, Vitt 16239 (ALTA). Southern Ogilvie Mtns., Tombstone Mtn., 64°28'N, 138°43'W. Vitt 16709 (ALTA). Keele Peak, 63°30'N, 130°27'W, Vitt 15763 (ALTA).

U.S.A. Alaska: St. Lawrence Island, Geist 1933 (DUKE). Healy Quadrangle, Alaska Range dist., Hermann 21294 (DUKE). Wrangel, Virginia Lake, Worley and Hamilton 8372 (SMS). Mt. McKinley National Park, Weber and Viereck 10153 (UC). Port Vita, Raspberry Group, Eyerdam 856 (UAC). Kodiak Island, Olga Bay, Looff E235 (CANM). Skagway Quadrangle, E of Haines, Hermann 21761 (CANM). Valdez Quadrangle, 19.2 km E on Lowe River, Hermann 21709 (CANM). Washington: Clallam Co., Lake Ozette, Olympic Peninsula, Becking 5306362 (WTU).

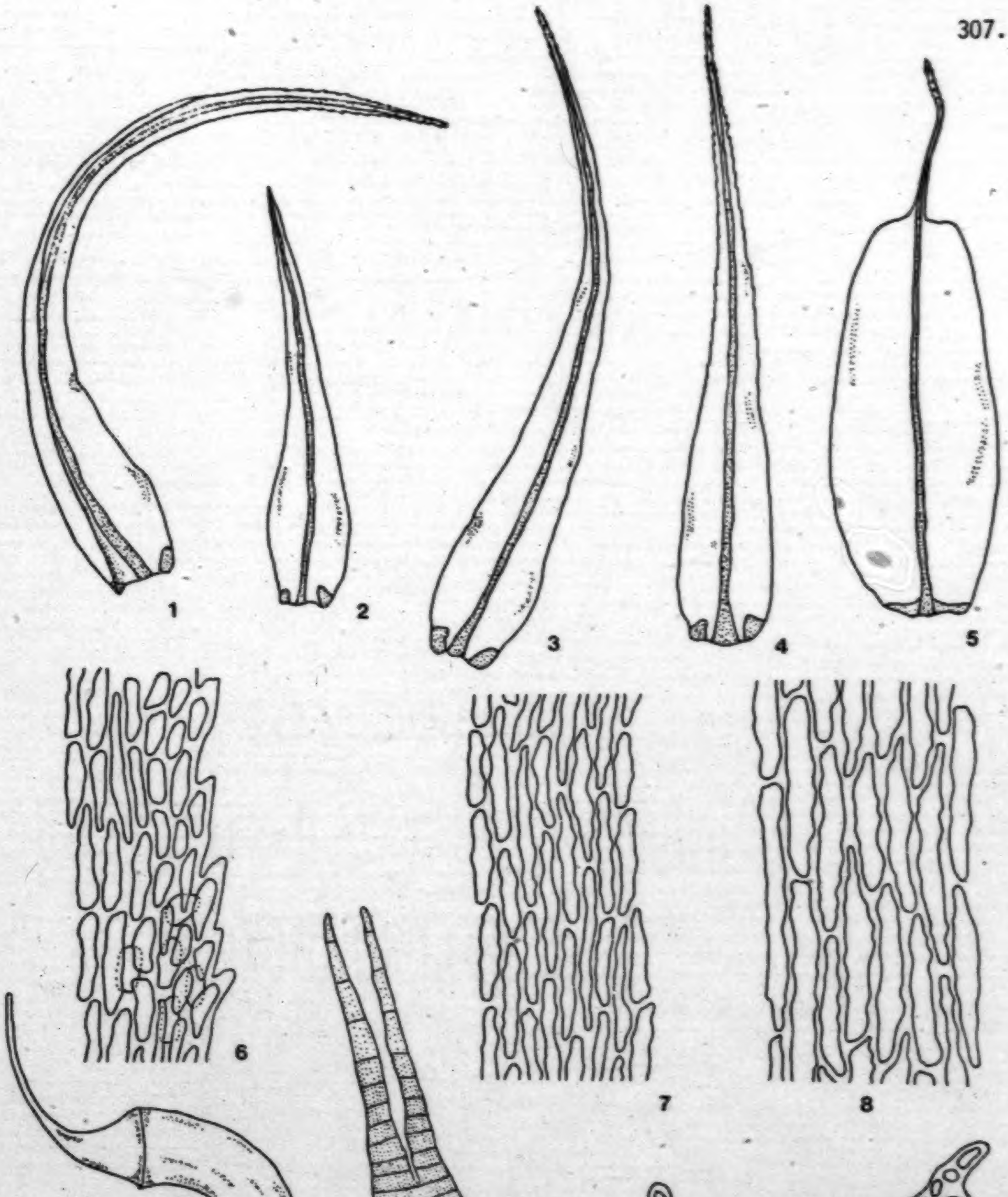
The distinguishing features of *D. majus* are several. The most obvious are the multiple setae and the large falcate-secund leaves that have a metallic luster. This luster gives the plants a dark, shiny appearance, quite different from the lighter shine that is found in other species. In addition, a transverse-section of a leaf shows two rows of guide cells (Fig. 63-13), a character state not found in any other Dicrana. In the same section, the costa can be seen to be somewhat convex and the upper row of cells may have larger lumens that differentiate them from the thicker walled stereids.

Dicranum majus is very distinct and seldom confused with other species. At times large specimens of *D. scoparium* may be mistaken for this species and, in such cases, a transverse-section is necessary to determine the correct identity. *Dicranum scoparium* does not have a double row of guide cells and it has lamellae on the abaxial costal surface (Fig. 68); whereas, *D. majus* does have the double row of guide cells and does not have lamellae. The northern forms of *D. majus* may lack the double row guide cells and be somewhat smaller in size than the more typical costal forms; however, they still have the characteristic metallic sheen found in the typical form and, with careful examination, should not be mistaken for any other species.

Nomenclature: *Dicranum majus* was described almost simultaneously by Smith and Turner in 1804. Both were valid publications and both cited the same Dillenius specimens as the type. These specimens are not available for examination; however, the figures pictured in

FIGURE 63. *Dicranum majus* Sm.

1-4 Stem leaves (9x)
5 Perichaetial leaf (9x)
6 Upper laminal cells (280x)
7 Median laminal cells (280x)
8 Basal laminal cells (280x)
9, 10 Capsules (10x)
11 Peristome tooth (180x)
12 Upper transverse-section (140x)
13 Median transverse-section (140x)



his *Historia Muscorum* (Dillineus, 1741) are precise drawings made from the actual specimens.

According to Sayre (1959), Smith's publication (Smith, 1804) was distributed to the general public on March 29, 1804, and Turner's publication (Turner, 1804) was similarly distributed on April 1, 1804. The situation is further complicated by the fact that Turner distributed 250 copies privately on March 20, 1804. As a result, many authors use this as the date of publication and cite Turner as the authority for names duplicated in these two publications. Crundwell (1970) examined this problem and felt that the privately distributed copies did not constitute valid publication and that the date of public sale (April 1, 1804) was the date of valid publication. As such, Smith's publication does indeed have priority, although only by two days, and Crundwell considered Smith to be the proper authority.

23. *Dicranum scoparium* Hedw., Spec. Musc. 126. 1801.

Type: Dillenius, Musc. T. 46, F. 16 (Specimen unavailable)

Dicranum dillenii Tayl., Ann. Mag. Nat. Hist. 12: 129. 1843.

Type: Newfoundland, Lambert. (Lectotype-FH!; Syntype-BM!)

Dicranum pallidum C. Müll., Syn. 1: 359. 1848.

Type: Sullivant, Musci Allegh. No. 155 (Lectotype-FH!).

Dicranum dipteroneuron C. Müll., Flora 70: 221. 1887.

Type: "Alaska, in valle Takhin, 20 Julio 1882. *Dr. Krause*" (not seen) *fide* Williams, 1913.

Dicranum howellii Ren. et Card., Rev. Bryol. 15: 70. 1888.

Types: *"Oregon in sylvis. Jam anno 1882 specimina circa Portland lecta amic Lesquereux misit; serius mense Martio 1888 Th. Howell legit."* (Syntype-F!).

Dicranum angustifolium Kindb. *in* Macoun, Bull. Tor. Bot. Club 17: 86. 1890.

Type: "On logs and damp rocks, frequent in British Columbia from the coast to the Gold Range, 1889". (Lectotype-S!; Syntype-CANM!).

Dicranum scopariforme Kindb., Ottawa Nat. 2: 154. 1889.

Types: "Described from specimens found by *Dr. G.M. Dawson* at bottom of canyon below *bridge, Elk River,* Rocky Mountains, but also found in McKay's Woods, Ottawa, at the base of trees; also in Nova Scotia and Prince Edward Island." (Elk River: Lectotype-S!; MacKay's Woods: Syntypes-S!, CANM!).

Dicranum canadense Kindb. *in* Macoun, Bull. Tor. Bot. Club. 17: 87. 1890.

Type: "On rotten logs at Moodyville, Burrad Inlet, B.C., April 29, 1889". (Lectotype-S!).

Dicranum consobrinum Ren. et Card., Bot. Gaz. 15: 39. 1890.

Type: Minnesota, Comm. *J. Henry* (Isotype-NY!)

Dicranum bonjeanii spp. *columbiae* Kindb., Bull. Tor. Bot. Club. 17: 86. 189.

Type: "Damp woods, by the borders of ponds, Cedar Hill, near Victoria, 1887; and on Campbell Hill, Cache Creek, B.C., ait. 2500 feet, May 25, 1875 (Macoun)." (Lectotype-S!).

Dicranum columbiae (Kindb.) Ren. et Card., Rev. Bryol. 19: 77. 1892.

Dicranum congestiforme C. Müll. et Kindb. *in* Macoun et Kindb. Cat. Can. Pl. 6: 29. 1892.

Type: "On damp rocks on the east side of Lake Mara at Sicamous, B.C., July 3, 1889." (Lectotype-S!).

Dicranum plano-alare C. Müll. et Kindb. *in* Macoun et Kindb., Cat. Can. Pl. 6: 31. 1892.

Type: "On earth at the mouth of the Illecillewaet Cañon, near Revelstoke, B.C., May 18, 1890." (Isotype-CANM!).

Dicranum subpalustre C. Müll. et Kindb. *in* Macoun et Kindb., Cat. Can. Pl. 6: 33. 1892.

Types: "On earth on rocks at Hector, Rocky Mountains; on rocks at Deer Park, Lower Arrow Lake." (Lectotype-S!). "Columbia River, June 18, 1890." (Syntype-S!).

Dicranum undulifolium C. Müll. et Macoun *in* Macoun et Kindb., Cat. Can. Pl. 6: 32. 1892.

Type: "On earth near Fort Rupert, Vancouver Island, 1885. (Dawson)." (Isotype-US!)

Dicranum kindbergii Paris, Index Bryol. 356. 1895. *Nom. illeg. incl. spec. prior.*

Dicranum hyalinum Kindb. *in* Röll, Hedwigia 35: 61. 1896

Type: "Yellowstone Nat. Park, Wyoming 7000'. Unter No. 1442 (Röll) als *D. scoparium* Hedw." (Lectotype-S!).

Dicranum perichaetiale Kindb. *in* Röll, Hedwigia 35: 61. 1896

Type: "Wash. Cascaden, Easton cfr. No. 554 exp. als *D. scoparium* Hedw. var. *paludosum* Sch. cfr." (Lectotype-S!).

Dicranum roellii Kindb. *in* Röll, Hedwigia 35: 60. 1896.

Type: "Vancouver Isl. Victoria" coll. Röll. (Lectotype-S!; Isotype-CANM!).

Dicranum bonjeanii var. *alatum* Barnes, Bot. Cent. 44: 386. 1890.

Types: "Illinois: Chicago (Dr. J. Röll, 1888). Wisconsin: Madison (Cheney and True). W. Minnesota: Cedar Lake, near Montevideo, Chippewa county (J.M. Holzinger, 1901)." (not seen) *fide* Williams, 1913.

Dicranum alatum (Barnes) Card. et Thér., Bot. Gaz. 37: 364. 1904.

Dicranum subscoparium Kindb., Rev. Bryol. 32: 35. 1905.

Types: "Canada: B.C., 5200-7500 ft. 1904, Macoun." (Lectotype-S!; Isosyntypes-S! CANM!).

Cecalyphum scoparium P.-Beauv., Prod. 51. 1805. *Nom. illeg. incl. gen. prior.*

Dicranodon scoparium Béheré, Musc. Rothom. 27. 1826. *Nom. illeg. incl. gen. prior.*

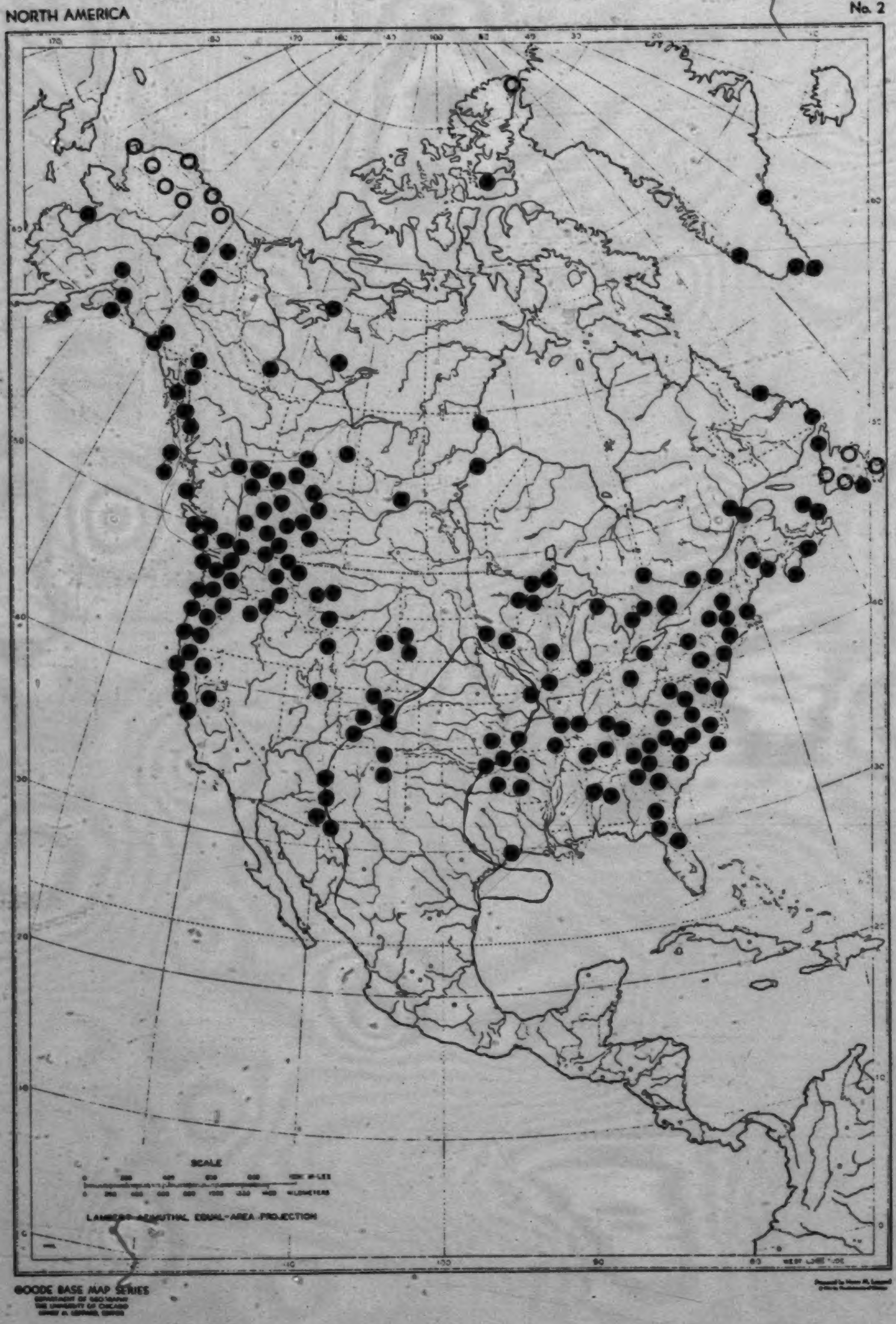
Plants in loose mats, 2 to 15 cm tall, light-green to dark-green, growing on humus or soil, rarely on decaying wood. Stems moderatley tomentose, tomentum white to brown. Leaves when dry falcate-secund to straight, erect or spreading, similar when moist, seldom undulate, 4.0-8.0 (12) mm long, broadly lanceolate to long-lanceolate, tapering to an acute apex, slightly tubulose or rounded, not keeled, smooth on both laminal surfaces; margins entire, or serrate to toothed in upper 1/2; costa narrow, (75) 85-110 μm wide just above alar region, subpercurrent to excurrent, with 2 to 4 unistratose lamellae on the abaxial surface, each lamellae consisting of 1 to 4 cell layers and extending from leaf tip to 1/2 to 2/3 the length of the leaf, lamellae rarely absent; costa in median transverse-section showing 4 to 6 guide cells and 2 stereid bands, both bands disappearing in the apex, abaxial layer of external cells differentiated from stereids by large lumens when lamellae are absent, the adaxial layer of external cells not differentiated; alar cells brown or opaque, bistratose, thin-walled, not extending to costa; basal cells above alar region elongate, pitted, (55) 75-110 μm long, thick-walled, median cells similar, 45-70 (85) μm long, upper cells similar, (30) 40-50 (65) μm long, (5.0) 8.0-15 (20) μm wide. Perichaetial leaves shorter than stem leaves, innermost ones emarginate to abruptly narrowed (or rarely gradually tapered) to a subulate tip.

Dioicous, male plants dwarfed and growing on tomentum of female plants. Monosetous, or rarely 2 or 3 setae per perichaetium, 1.5-3.5 cm long, yellow to dark-brown. Capsules yellow to brown, 1.5-4.0 mm long, curved, ribbed, not strumose, neck short; exothecial cells rectangular to linear, pitted or not pitted, 25 to 65 μm long, thin-walled; stomates few in one loose row at base of capsule, 32-45 μm;

rostrate, curved or straight, 1.5-2.5 mm long; annulus absent; peristome teeth orange to red, vertically striate, about 0.5 mm long, 90-110 µm wide at base, divided half way down into 2 or 3 (occasionally 4) segments; spores green to brown, finely papillose, (13) 15-22 µm. Chromosome number, n=11, 12 (11 + x + y).

Habitat and Distribution (Fig. 64): The habitat range of *D. scoparium* is quite broad, with the species being found in moist to dry forests, around mires, along streams, and in open tundra. It grows on soil, humus logs, and occasionally over rocks, and in each case it can be very luxurient. It is the most cosmopolitan member of the genus *Dicranum*; almost ubiquitous in northern temperate latitudes of both North America and Eurasia and it is encountered from the arctic through the subtropics. It is reported from New Zealand (Allison, 1952; Sainsbury, 1955) and the possibility exists that this disjunction might be the result of horticultural introductions that contained fragments of *D. scoparium* attached to them; however, this is unlikely as the New Zealand specimens were collected at an altitude over 1200 metres on hummocks in a swampy alpine area, hardly where one would expect introductions. The specimens I have seen from New Zealand are not unlike forms found in similar habitats in North America. It is probable that *D. scoparium* is more widespread in the southern hemisphere than indicated by collected specimens. A more detailed examination of the southern floras with empahsis upon *Dicranoloma*

FIGURE 64. The North American distribution of *Dicranum scoparium* Hedw.


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

(members of which *Dicranum scoparium* might be taken for) would be necessary to determine this.

In North America, *D. scoparium* occurs in all habitats except the most extreme ones like the arid deserts and grasslands. It is found in the high arctic from northern Alaska to Devon Island and Greenland; however, it is not common in these areas, and is replaced by such other species as *D. angustum*, *D. amannii*, and *D. spadiceum*. The more southern limits in North America are defined by the southern extent of the coastal forest in California, while in the Rocky Mountains, the distribution extends into the highlands of Mexico.

Selected Specimens Examined: EXSICCATI. Austin, Musci Appal. 85 (CANM), 86 (CANM), 87 (CANM), 88 (CANM), 89 (CANM), 90 (CANM), 91 (CANM), 473 (CANM). Baker, Pacific Slope Bryophytes 584 (UC, US), 739 (UC). Drummond, Musci Amer. (Rocky Mtns.) 80 (CANM). Grout, Hand-Lens Mosses 28 (DUKE). Grout, North American Musci Perf. 5 (DUKE, CANM). Holzinger, Musci Acroc. Bor. Amer. 7 as *D. palustre* var. (NY, CANM), 55 (CANM), 133 (NY, CANM), 176 (NY, UC, F, CANM), 205 as *D. palustre* (NY, DUKE, CANM), 206 (UC, CANM), 334 as *D. bonjeanii* var. (NY, CANM), 354 as *D. bonjeanii* var. (NY, UC, F, CANM), 390 as *D. bonjeanii* var. (NY, US, CANM), 607 (CANM), 611 (NY). Macoun, Can. Musci 42 (UC, CANM, NY), 43 (UC, NY, CANM), 363 (NY, CANM). 405 (NY, UC), 406 (NY, CANM), 407 (UC, CANM, NY), 408 (US, UC, NY, CANM), 409 (UC, US, NY), 556 (NY, UC), 561 (US, NY). Renauld and Cardot, Musci Amer. Sept. 10 (FH, CANM), 11 as *D. consobrinum* (FH), 275 as *D. howellii* (FH, CANM), 359 (FH, CAN), 360 as *D. scopariforme* (FH, CANM). Small, Mosses Southern U.S. 18 (NY, FH, DUKE, CANM), 66 as *D. bonjeanii* (NY). Sull. and Lesq., Musci Bor. Amer. (ed. I) 59, 60, 61, 62 (NY, FH), 66 as *D. palustre* (NY, FH). Sull. and Lesq., Musci Bor. Amer. (ed. II) 75, 76, 77, 78 (NY, FH), 83 as *D. palustre* (NY, FH).

CANADA. Alberta: Ft. McMurray, 2 km S of town along Athabasca River, Peterson 4836 (ALTA). Jumping Pound Creek, McCutcheon 213 (LAF). Mountain Park Area, 117°22'W, 52°59'N, Peterson 805 (ALTA). Battle Lake, W of Pigeon Lake, Peterson 1158 (ALTA). Rocky Mtn. House, about 50 km SW of the town, Peterson 3288 (ALTA). Jasper National Park, Mt. Edith Cavell, Peterson 3526 (ALTA). British Columbia: New Westminister, Hill 739 (US). Queen Charlotte Islands, Schofield and Boas 18998 (DUKE). About 440 km N of Ft. St. John, 58°10'N, 122°50'W, Peterson 2956 (ALTA). Powell Lake, Flowers 7650 (COLO). Vancouver Island, Victoria, Flowers 7600 (COLO). Azouzetta Lake, 55°22'N, 122°37'W, Peterson 3155 (ALTA). Near Jasper National Park, 121°18'W, 53°49'N, Peterson 3208 (ALTA). Manitoba: Ft. Churchill, Goose Creek, Steere 7197 (DUKE). Newfoundland: Labrador, Hopedale, Wickes Aug. 6, 1940 (DUKE). Labrador, Battle Harbour, Macoun Sept. 5, 1891 (CANM). Eddies Cove West, 50°42'N, 57°11'W, Tuomikoski 4467 (CANM). Nova Scotia: Halifax, Macoun 44 (CANM). Victoria Co., Cape Breton Island, Schofield 6105 (TENN). Sable Island, Macoun 47 (DUKE). Ontario: Bear Island, Lake Temajama, Cain 263 (DUKE). Bruce Co., Pike's Bay, Moxley 1732 (DUKE). Gatineau Park, Luskville Falls, Peterson 2391 (ALTA). Quebec: Chelsea, Macoun 37 (DUKE). Mt. Shefford, Fabius 2215 (DUKE). Murray Bay, LeGill 1215 (SMS). Saskatchewan: Drinking Lake, Welsh 560 (DUKE). Northwest Territories: Great Bear Lake, Sawmill Bay, Steere 10376 (SMS). Devon Island, Truelove Lowland, Peterson 2460 (ALTA). Yellowknife, Ingraham Trail, 62°34'N, 114°00'W, Jasieniuk 2259B (ALTA). Yukon Territory: Dawson City, Bonanza Creek, Peterson 1376 (ALTA). Bonanza Creek, Macoun 33a (US).

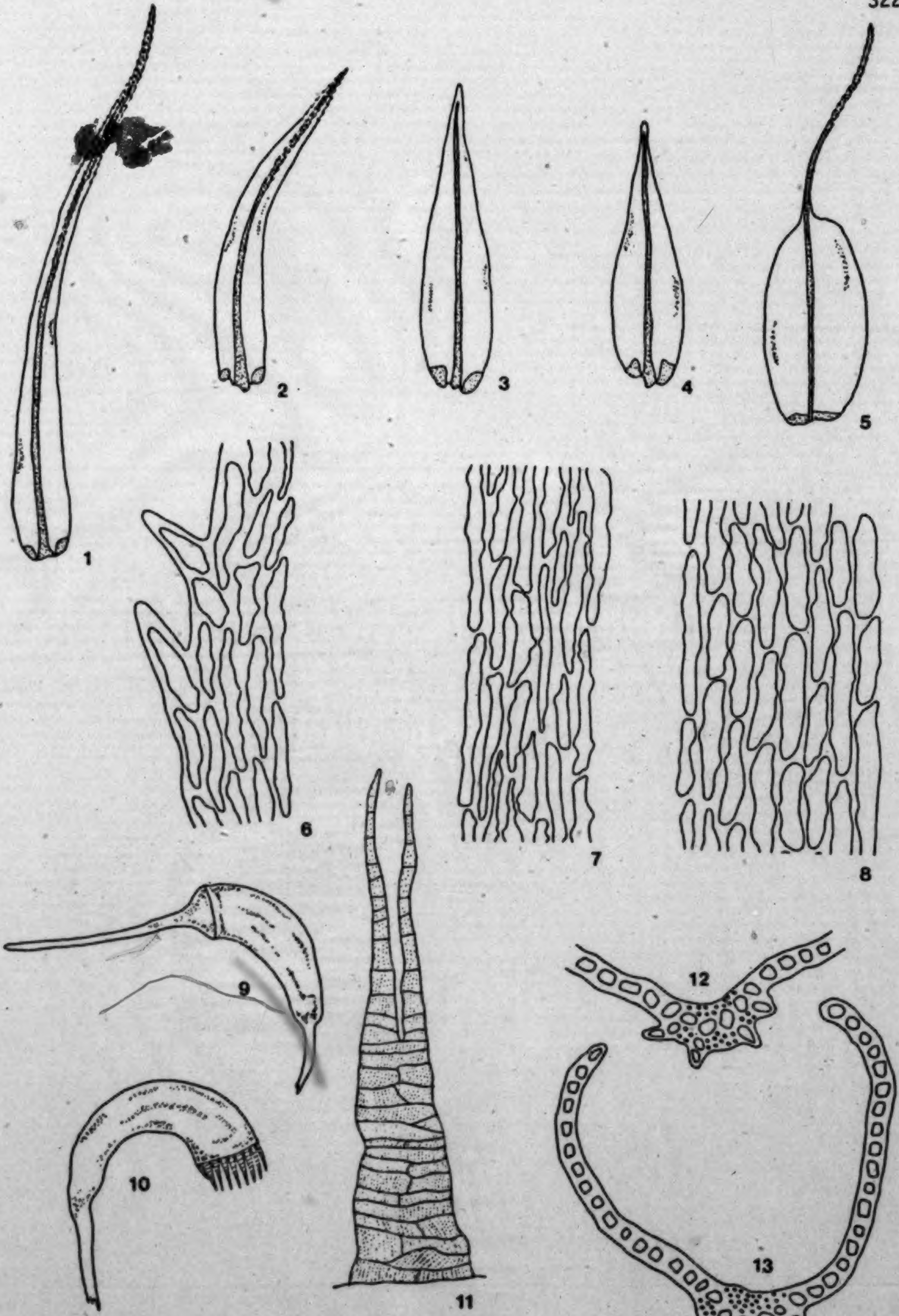
U.S.A. Alaska: Glacier Bay, Worley and Boas 10184 (SMS). Mt. McKinley National Park, Vierek 3218 (COLO). Kodiak Island, Kodiak, Hultén April 27, 1932 (DUKE). Alabama: Tuscaloosa Co., Hurricane Creek, Harper 3149 (DUKE). Auburn, Baker Oct. 15, 1896 (UC). Leeds Evanson 712 (US). Arizona: Apache Co., Phelps Botanical Area, Phillips 3074 (ARIZ). White House Canyon, Bartram 9 (ARIZ). Chocise Co., Fly's Peak, Weber and Shushan 10619 (UC). Arkansas: Franklin Co., White Rock Mtn., Iltis April 19, 1953 (TENN). Montgomery Co., Mt. Ida, Redfearn 47044 (TENN). California: Trinity Co., Canyon Creek, Norris 8030 (HSC). Del Norte Co., Stony Creek NE of Gasquet, Peterson 995 (ALTA). Humboldt Co., 8 km W of Willow Creek, Peterson 1014 (ALTA). Placer Co., Ionesca Aug. 22, 1934 (CAS). Colorado: Douglas Co., Devils Head Mtn., Weber 77491 (COLO). Grand Co., St. Louis Creek, Bowers 66477 (DUKE).

Pithin Co., Aspen, *Weber* *B10925* (LAF). *Connecticut*: New London Co., Vicinity of Norwich, *Holdridge*, summer and fall, 1946 (MIN). Hamden, *Evans* June, 1890 (US). *Florida*: Columbia Co., O'Leno State Park, *Anderson* and *Crum* *13644* (DUKE). *Georgia*: Irwin Co., Irwinville, *Hermann* *10066* (DUKE). Walton Co., *Small* July 1893 (US). DeKalb Co., Stone Mtn., *Small* *9668* (DUKE). *Idaho*: Lewis Co., Winchester, *Cooke* *24979* (F). Kootenai Co., Hope, *Sandberg* *1109* (US). Bonner Co., Dickensheet Campground, Priest Lake, *Peterson* *1111* (ALTA). *Illinois*: Athens, *Hall* *40* (F). *Indiana*: Porter and Lake Co. line, Lake Michigan, *Habeeb* April 4, 1948 (CAS). *Kentucky*: Bullitt Co., 8 km NE of Shephardville, *Crum* *2603* (CANM). Whitley Co., Cumberland Falls State Park, *Norris* *62617a* (TENN). *Maine*: Penobscot Co., Lower Penobscot Valley, *Fernald* 92 (MIN). Acadia National Park, *Schnasberger* and *Wayne* Dec. 7, 1940 (DUKE). *Massachusetts*: West Andover, *Thompson* Oct. 7, 1923 (DUKE). *Maryland*: Somerset Co., Princess Anne, *Drouet* *3619* (UC). Bladenburg, *Leonard* *17894a* (US). *Michigan*: Emmet Co., 5 Mile Creek, *Snider* *889* (MICH). *Minnesota*: Chippewa Co., Cedar Lake, *Holzinger* June 18, 1901 (MIN). Cook Co., Susie Island, *Olson* *702* (MIN). *Missouri*: Clark Co., Athens, *Steyermark* *28701* (UC). St. Francis Co., Mountain Lake, *Kellogg* May 1, 1927 (COLO). Webster Co., James River, *Redfearn* *4271* (TENN). *Montana*: Park Co., Gallatin National Forest, *Griffin* *C400* (LAF). Flathead Co., Jackson Creek, *Bailey* *15* (UC). Little Beet Mtns., Baker, *Leinberg* *781* (CAS). *New* *Hampshire*: Lebanon, *Holcombe* *442* (DUKE). *New* *Mexico*: Taos Co., Wheeler Peak, *Hermann* *23976* (DUKE).

Pecos River National Forest, Standley 3996 (DUKE). New York: Green Co., Tannersville, Vail 88 (MIN). North Carolina: Macon Co., Highlands, Anderson 9090 (DUKE). Wilkes Co., Blue Ridge Parkway, Anderson 7533 (DUKE). Mitchell Co., Crabtree Meadows, Anderson and Jones 9439 (DUKE). Ohio: Painsville, Werner July 20, 1896 (MIN). Oklahoma: McCurtin Co., Whitehouse 24472 (US). Deleware Co., Redfearn 20979 (SMS). Haskell Co., Redfearn 19770 (SMS). Oregon: Tillamook Co., Neshowin Forest Camp, Young 266 (LAF). Wallowa Co., Imnaha River, Hermann 18936 (COLO). Umatilla Co., LaGrande at Frazier Campground, Peterson 1083 (ALTA). Pennsylvania: Lancaster and Lebanon Co. line, Mt. Hope, Small, Dec. 31, 1891 (MIN). Bradford Co., 1.6 km NE of Durell, Webster 68079 (TENN). South Carolina: Lancaster Co., Taxahaw, Huntley 118 (DUKE). Oconee Co., Clemson College, House 1693 (DUKE). South Dakota: Pennington Co., Whitehouse 25266 (US). Texas: Sabine Co., Yellowpine, Reese 9741 (LAF). Tennessee: Wilson Co., Lebanon, Whitehouse 26843 (US). Knoxville, Ruth 10 (MIN). Utah: Summit Co., Mirror Lake, Flowers 7395 (COLO). Duchense Co., Flowers 9576 (COLO). Vermont: Windsor Co., Weston, Patch 2 (DUKE). Ruthland Co., Pico Peak, Holcombe 398 (DUKE). Virginia: Appatomax Co., Appatomax, Beaudry *et al.* 2 (DUKE). Shenondoah National Park, Book Aug. 12, 1966 (US). Washington: Thurston Co., 16 km E of Yelm, Peterson 955 (ALTA). King Co., Grass Lake, Eyerdam 513 (WTU). Callam Co., Sequin State Park, Correll and Correll 25893 (COLO). West Virgina: Randolph Co., Red run, Gray 7618 (MIN). Wisconsin:

FIGURE 65. *Dicranum scoparium* Hedw.

1-4	Stem leaves (9x)
5	Perichaetial leaf (9x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells
9,10	Capsules (10x)
11	Peristome tooth (180x)
12	Upper transverse-section (140x)
13	Median transverse-section (140x)



Madison, True 892 (DUKE). Bayfield Co., Flowers 9887 (COLO). Ashland Co., Madelaine Island, Andrews 10023 (COLO). Wyoming: Teton Co., Cascade Canyon, Redfearn 11720 (LAF). Johnson Co., Bighorn National Forest, Weber *et al.* B46663 (COLO). Yellowstone National Park, Norris Geyser Basin, Frye Aug. 14, 1925 (WTU).

The plasticity of *Dicranum scoparium* has undoubtedly led to more confusion than in any other taxon in the genus. There have been at least twenty species described that can be related directly to the North American flora and, no doubt, many others that do not. Many of these taxa do appear distinct when examined separately; however, when the entire complex is studied many intergrading characters and forms become apparent.

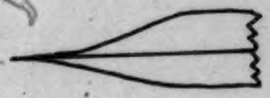
The most interesting of these "species" are represented by *D. howellii* (Fig. 11-2) on the west coast, *D. consobrinum* of the Minnesota region, *D. alatum* (Fig. 11-4) of the east coast, and *D. undulifolium* (Fig. 12-1) of the northwestern part of Canada. The distinctive features of each are not significant enough to warrant specific recognition. Typically *D. scoparium* has, in addition to long upper cells, 4 lamellae on the abaxial surface of the costa, non-undulate leaves that are falcate-secund, a slightly excurrent costa, and inner perichaetial leaves that are abruptly acuminate. It is variation in this last character that led to the partial acceptance of *D. howellii* and to the description of *D. consobrinum*, with the former having inner perichaetial leaves that are gradually acuminate and the latter with emarginate or slightly apiculate perichaetial leaves. In both cases, intergrading forms are not uncommon and, at times, can be found in the same mat. Figure 66 represents the variation that may be found in the perichaetial leaves of *D. scoparium*. All of these leaves are slightly longer and wider than the normal stem leaves, and at maturity they envelop the base of the seta. Figure 66-1 represents the more common state found in *D. scoparium* by having an abrupt attentuation from the relatively straight sides to the subulate tip. The west coast form that has been referred to as *D. howellii* has perichaetial leaves like those if Figs. 66-2 and 66-3 which have a rather gradual attentuation from the sides to the tip. There are a number of west coast specimens that have these types of leaves and could easily be called "*D. howellii*", but on the other hand, there are specimens from the west coast that have perichaetial leaves of both types. Since this character is the only one that has been suggested to separate these two "species" and I have been unable to find other characters, I choose to consider the western "*D. howellii*" as a modification of *D. scoparium*. Figure 66-4 and 66-5 represent perichaetial leaves found in what has been described as *D. consobrinum*. The species has never received wide acceptance as the only difference between it and *D. scoparium* is the emarginate (Fig. 66-5) or apiculate (Fig. 66-4) perichaetial leaves. As in "*D. howellii*" these are variable and emarginate perichaetial leaves may be found, at times,

FIGURE 66. Variation in the apices of inner perichaetial leaves of *Dicranum scoparium* Hedw.

1. An abruptly acuminate apex of the type found in most specimens.

2 and 3. Gradually acuminated apices attributed to the "*D. howellii*" form.

3 and 4. Apiculate and emarginate apices attributed to the "*D. consobrinum*" form.



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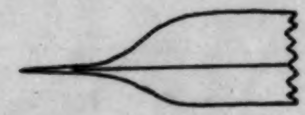

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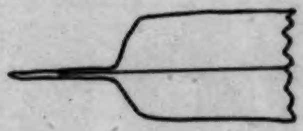

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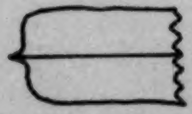

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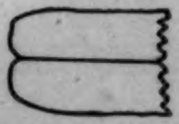

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among populations that have the typical leaf as seen in Fig. 66-1. Again, I do not consider a single character, that varies even slightly, to be sufficient to justify the acceptance of a species, especially when that species would be segregated from a highly polymorphic group.

Dicranum alatum (Fig. 11-4) and *D. undulifolium* (Fig. 12-1) forms have caused a partial acceptance of the European *D. bonjeanii* (Fig. 11-3) concept in North America since they both have shorter and straighter leaves, fewer lamellae (usually two or less) and slightly undulate leaves. Figure 67 shows the leaf shapes characteristic to these forms and indicates the probable lines of intergradation between them. As shown, the "*D. bonjeanii*" type of leaf is probably derived from at least three different pathways. The "*D. alatum*" form, normally found in eastern North America, is nothing more than *D. scoparium* with shorter leaves. The leaves are still falcate-secund and serrulate near the apex as those of typical *D. scoparium*, lamellae are present on the abaxial costal surface although the outer two may be less prominent than the inner two (Fig. 68). In addition, the shorter, falcate-secund state may cause the leaves to be slightly concave. The form "*D. undulifolium*" is normally found in the north, being fairly common in northern Alberta and British Columbia. The leaves of this form are straight, erect and slightly undulate, and the lamellae on the abaxial surface may be reduced or represented only by several enlarged cells in the abaxial costal layer (Fig. 68). Many other

FIGURE 67. Variation in leaf forms of *Dicranum scoparium* Hedw. and *Dicranum polysetum* Sw. Arrows indicate lines of intergradation that result in forms called "*Dicranum bonjeanii*".

1. Leaf of typical *D. scoparium* Hedw.
2. Leaf of the "*D. alatum*" form of *D. scoparium* Hedw.
3. Leaf of typical *D. polysetum* Sw.
4. Leaf of the "*D. undulifolium*" form of *D. scoparium* Hedw.
5. Leaf of "*D. bonjeanii*" form.

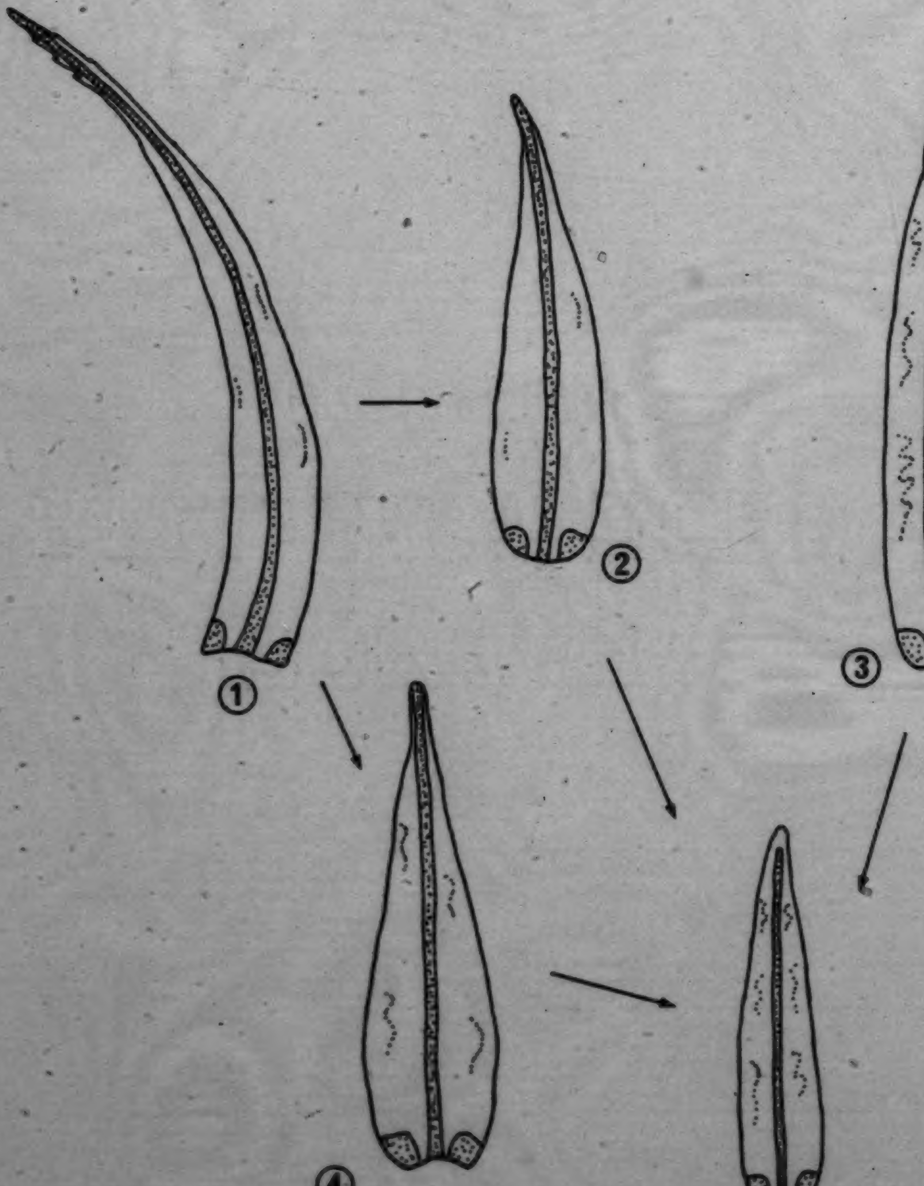
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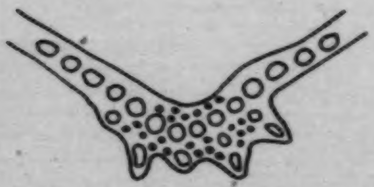
FIGURE 68. Variation of abaxial lamellae in *Dicranum scoparium* Hedw.

1. Typical *D. scoparium* with four lamallae
2. "*Dicranum undulifolium*" form with enlarged cells in the abaxial costal layer.
3. "*Dicranum elatum*" form with two prominent lamellae and two reduced lamellae.
4. "*Dicranum bonjeanii*" form with two lamellae.



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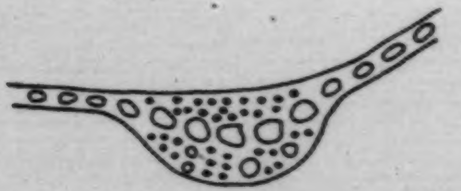

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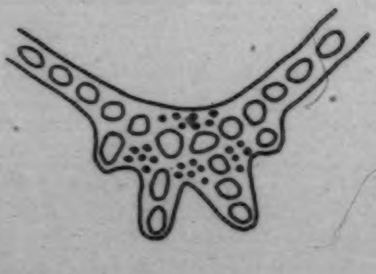

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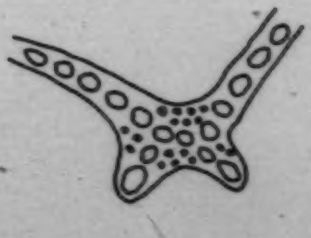

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specimens are intermediate between these forms and therefore difficult to position. Similiar specimens exist between the typical *D. scoparium* and the "*D. alatum*" form. It is for this reason that I consider these forms to be within the species concept of *D. scoparium*.

In addition to the forms "*D. alatum*" and "*D. undulifolium*", reduced forms of *D. polysetum* may be taken for *D. bonjeanii*. Crum (1973) stated, "*D. bonjeanii*" is "...a pigeon hole for convergent forms of *D. scoparium* and *D. polysetum*". Like *D. bonjeanii*, *D. polysetum* has straight, undulate leaves, 2 to 4 lamellae (usually 2), and serrulate to serrate margins. In its typical form, *D. polysetum* is unmistakable, however reduced, sterile forms often appear close to the descriptions of *D. bonjeanii*. I am convinced that *D. bonjeanii* does not occur in North America but it is possible that it is a good species in Europe and consequently, I have not included the name in my list of synonomy.

The "*D. undulifolium*" form is also responsible for reports of *D. leioneuron* (a species of ombrotrophic bogs of the Canadian Maritime Provinces) in western Canada. This form occasionally produces attenuated apices in a manner similar to that in *D. leioneuron*; however, the leaves on the western specimens have slightly serrulate tips while those of *D. leioneuron* are entire. In addition, the "*D. undulifolium*" form occurs in rocky areas and around calcareous fens, not in ombrotrophic bogs.

In summary, any North American *Dicranum* with long upper cells and abaxial lamellae or remnants of lamellae (with the exceptions of the obvious *D. polysetum*, the cucullate *D. amannii* and *D. leioneuron* of ombrotrophic bogs) should be included under the concept of the polymorphic and troublesome *D. scoparium*. Two additional species that lack lamellae and might occasionally cause confusion when dealing with this group are *D. angustum* (common in the north) and *D. rhabdocarpum* (endemic to the Rocky Mountains south of Wyoming). The former has small capsules, an annulus, and well developed stereids while the latter has erect to semi-erect capsules and only partially bistratose alar cells.

23. *Dicranum leioneuron* Kindb. *in* Macoun, Bull. Tor. Bot. Cl. 16: 92. 1889.

Type : "In damp woods on McNab's Island near Halifax, Nova Scotia. June 19, 1883. John Macoun". (Not seen). (Neotype: Halifax, Nova Scotia, 1888. John Macoun-S!).

Plants in loose mats, up to 10 cm tall, light-green, growing on humus or peat in ombrotrophic bogs. Stems lightly tomentose, tomentum brown. Leaves when dry straight, erect or slightly twisted, when moist straight and erect, slightly undulate, 4.0-8.5 mm long, long lanceolate, tapering to an acute tip, not keeled, smooth on both laminal surfaces; margins entire or serrate in upper 1/4; costa narrow, 95-110 µm wide just above alar region, subpercurrent, lamellae rarely present in upper 1/4 of leaf, enlarged cells occasionally present on abaxial costal surface; costa in median transverse-section showing 3 to 5 guide cells and two stereid bands, both bands disappearing in apex; neither abaxial or adaxial layer of external cells differentiated from stereid cells except for occasional enlarged cells in abaxial layer; alar cells brown, bistratose, thin-walled, not extending to costa; basal cells above alar region rectangular, thin-walled, pitted, (40) 60-80 µm long; median cells similar, 40-65 µm long; upper cells thick-or thin-walled, 40-50 µm long (4-6:1), pitted. Specialized attenuated stem tips usually present, 0.5 to 3.5 (5.0) cm long, leaves of attenuated tips shorter than stem leaves, 2.0 to 3.5 mm long, ovate to ovate-lanceolate, with a broadly acute apex; costa percurrent or subpercurrent, stereid bands absent; alar cells weak or absent; laminal cells similar to those of stem leaves. Perichaetial leaves slightly shorter than stem leaves, innermost ones abruptly narrowed to a subulate tip.

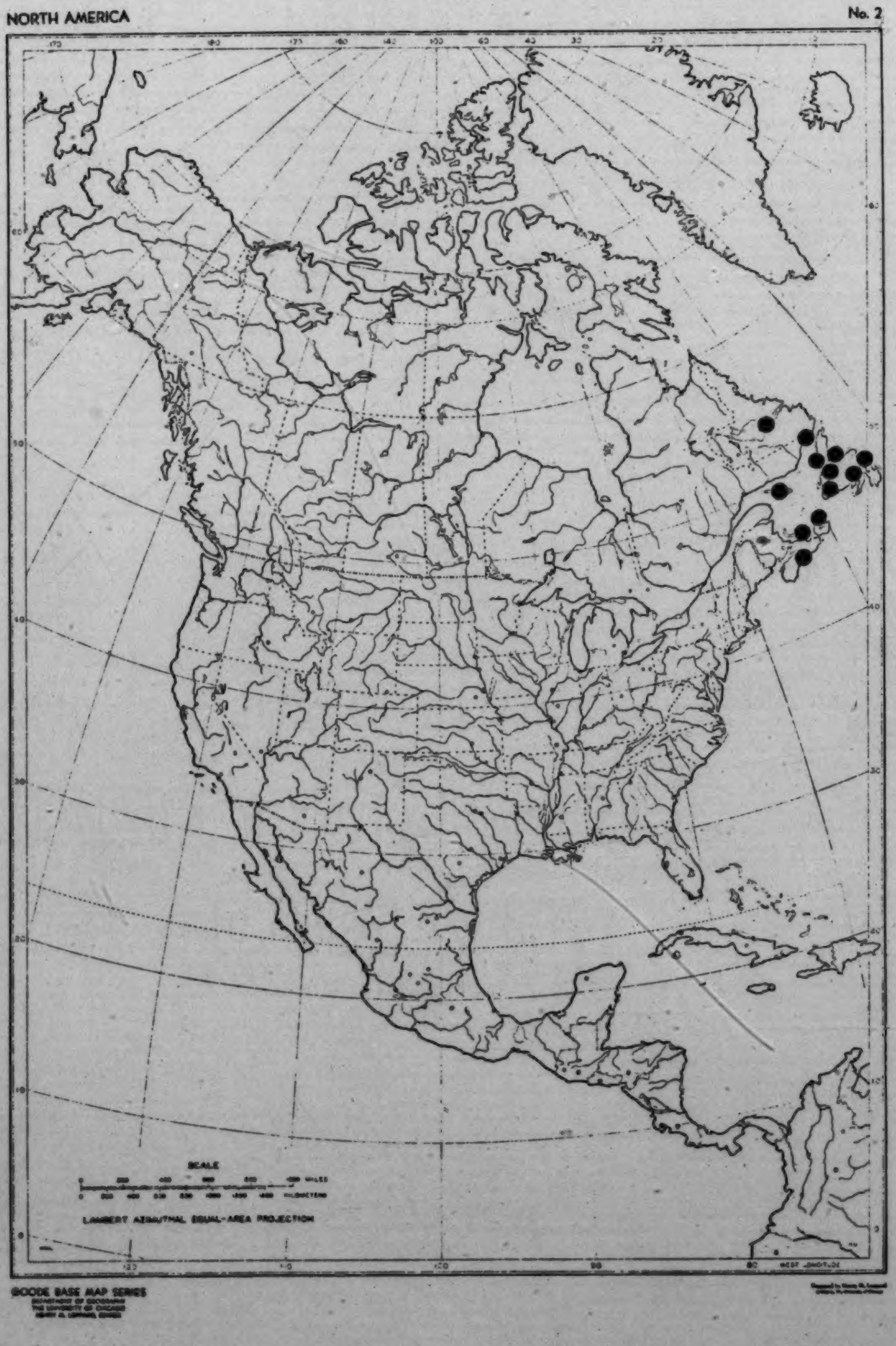
Dioicous, male plants not seen; monosetous, setae yellow to brown, 3.0-4.5 cm long. Capsules yellow to brown, 2.5-4.0 mm long, curved, ribbed, not strumose, neck short; exothecial cells rectangular, thin-walled, not pitted, 25-40 µm long; stomates few in one loose row at base of capsule, 28-31 µm long; opercula rostrate, about 2.5 mm long; curved or straight; annulus absent; peristome teeth orange to red, vertically striate, about 4.0 mm long

65-70 µm wide at base, divided almost to base into 2 or 3 segments, slightly cribbose; spores green, finely papillose, 19-23 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 69): The ecology of *Dicranum leioneuron* was studied by Ahti and Isoviita (1962) and the species was found to be restricted to sub oceanic regions, typically occurring in raised and blanket ombrotrophic bogs. Most often, the species grows in open bog situations on living *Sphagnum* hummocks, and according to Ahti and Isoviita (1962), the optimal conditions for this species are between those of *Sphagnum fuscum*, which grows above the water table, and *S. rubellum*, which usually grows in wet areas at the base of the hummocks. The average pH for these areas is about 3.5-4.0.

Specimens from western North America have been cited as *D. leioneuron*; however, those I have seen are forms of *D. scoparium*. They do possess flagellated shoots, but the shoot leaves are serrate instead of entire, and the plants in general are much more stunted than the typical material from Nova Scotia. My observations indicate that the species is restricted to the Canadian Maritime region on North America. It is also found in the British Isles, Scandanavia, Denmark, Estonia, and Latvia (Ahti and Isoviita, 1962; Ahti *et al.*, 1965).

FIGURE 69. The North American distribution of *Dicranum leioneuron* Kindb.


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

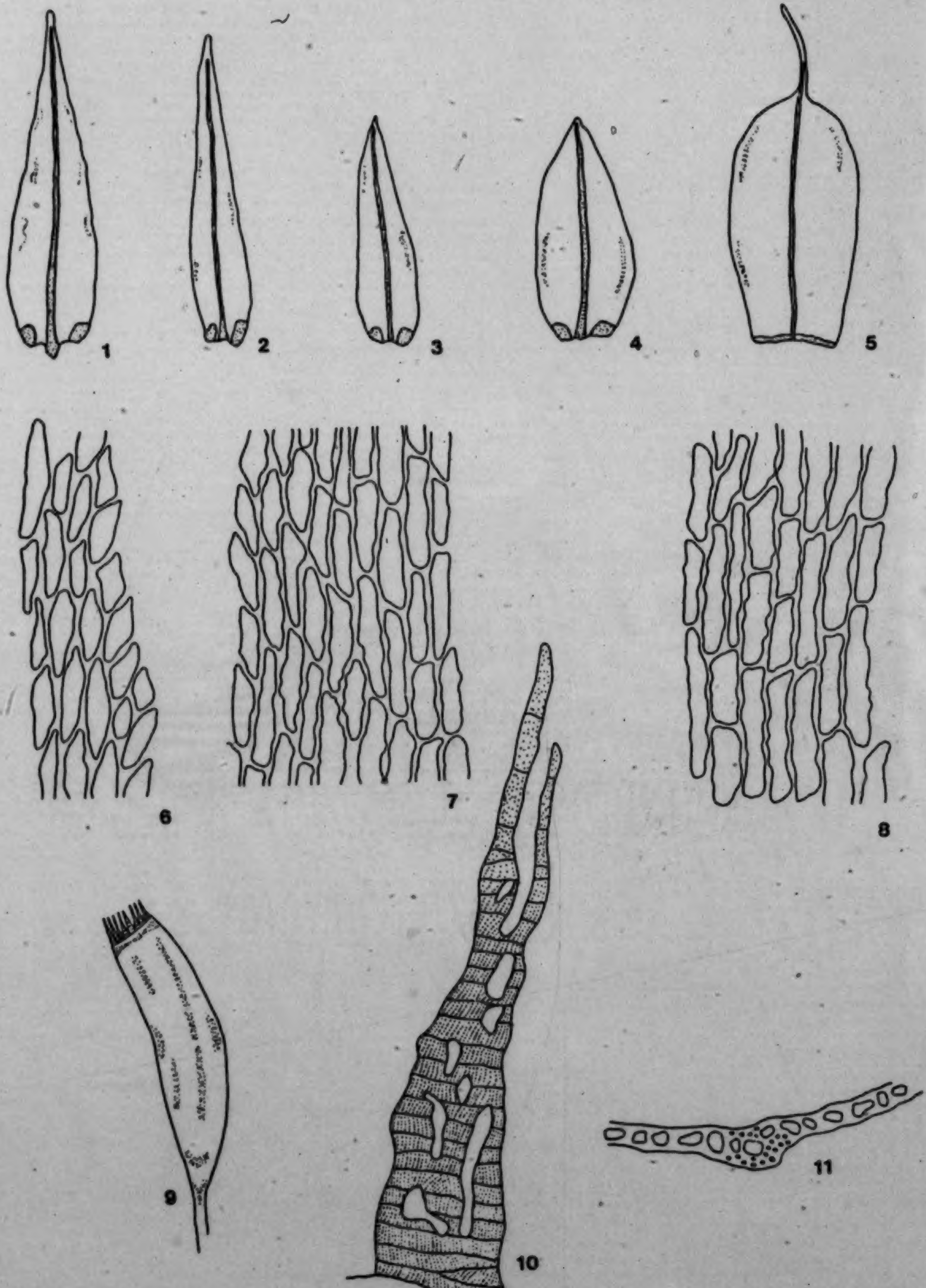
Selected Specimens Examined: CANADA. Newfoundland: South Branch, St. George's, 47°54'N, 58°53'W, Tuomikoski 2430 (CANM). Hogan's Pond, near Windsor Lake, 47°34'N, 52°54'W, Tuomikoski 283 (CANM). St. Barbe Bay, 51°08'N, 56°46'W, Tuomikoski 4344 (CANM). Ha-Ha Bay, White Bay, 51°30'N, 55°42'W, Tuomikoski 3667 (CANM). Nova Scotia: Halifax, 1888, Macoun (S). Cape Breton Highlands National Park, Ireland 11826 (CANM). Quebec: Anticosti Island, Salt Lake, 1883 Macoun (S). Prince Edward Island: Kings Co., 46°28'N, 62°13'W, Ireland 14109 (DUKE).

The distinguishing characters of *D. leioneuron* are few. The attenuated branch tips (Fig. 12-2) with short entire leaves and the very specific habitat of ombrotrophic bogs are the most important. No other Dicrana, in North America, has this combination of characteristics. In addition, the costa is fairly thin and has only 3 to 5 guide cells visable in median transverse-section (Fig. 70-11) while other species normally have 5 to 8 visable at a similar position in the leaf. *Dicranum scoparium* is the only species that *D. leioneuron* might be confused with since the former may lack lamellae (like *D. leioneuron*) and can have attenuated branch tips. In such cases the nature of the leaves on the attenuated tips and the habitat should separate them.

Nomenclature: The specimen cited in the original description as being collected on McNab's Island near Halifax, Nova Scotia, by

FIGURE 70. *Dicranum leioneuron* Kindb.

1-4	Stem leaves (14x)
5	Perichaetial leaf (9x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9	Capsule (10x)
10	Peristome tooth (180x)
11	Median transverse-section (140x)



John Macoun in 1883, is apparently lost or misplaced, as it is not in either Kindberg's herbarium at Stockholm or among Macoun's specimens at Ottawa. There is a specimen in Kindberg's herbarium from Halifax, Nova Scotia, that was collected in 1888 and cited by Ahti and Isoviita (1962) as a "topotype" since they too were unable to locate the original collection. Ahti and Isoviita point out that according to Macoun's catalog (Macoun and Kindberg, 1892), he only collected mosses in Nova Scotia during 1882 and 1883; therefore, the "Halifax, 1888" specimen may be the actual type, only mislabeled. According to Macoun's Autobiography (1922), he did return to Nova Scotia in 1888 for an agricultural convention and actually visited Halifax the next day. It is highly probable that he collected a few specimens during this trip, including the *D. leioneuron* specimen in question. If this is true, it would have been difficult for the specimen to be the one seen by Kindberg for the type description since 1888 is too close to the 1889 publishing date.

As a result, I must conclude that the original type is lost or misplaced and that the specimen in the Stockholm herbarium was actually collected in 1888 as the label states. Nevertheless, this specimen is from the type locality and was named by the author of the species, and should represent his concept ; therefore, I select it as a neotype.

24. *Dicranum rhabdocarpum* Sull., Mem. Am. Acad. Sci. II 4: 172. 1849.

Type: "Santa Fé, New Mexico, Mr. Fendler." (Holotype: FH-SULL!).

Orthodicranum rhabdocarpum (Sull.) Holz., Bryologist 28: 22. 1925.

Dicranum scoparioides Schimp. *in* Besch., Mem. Soc. Sc. Nat. Cherbourg 16: 164. 1872.

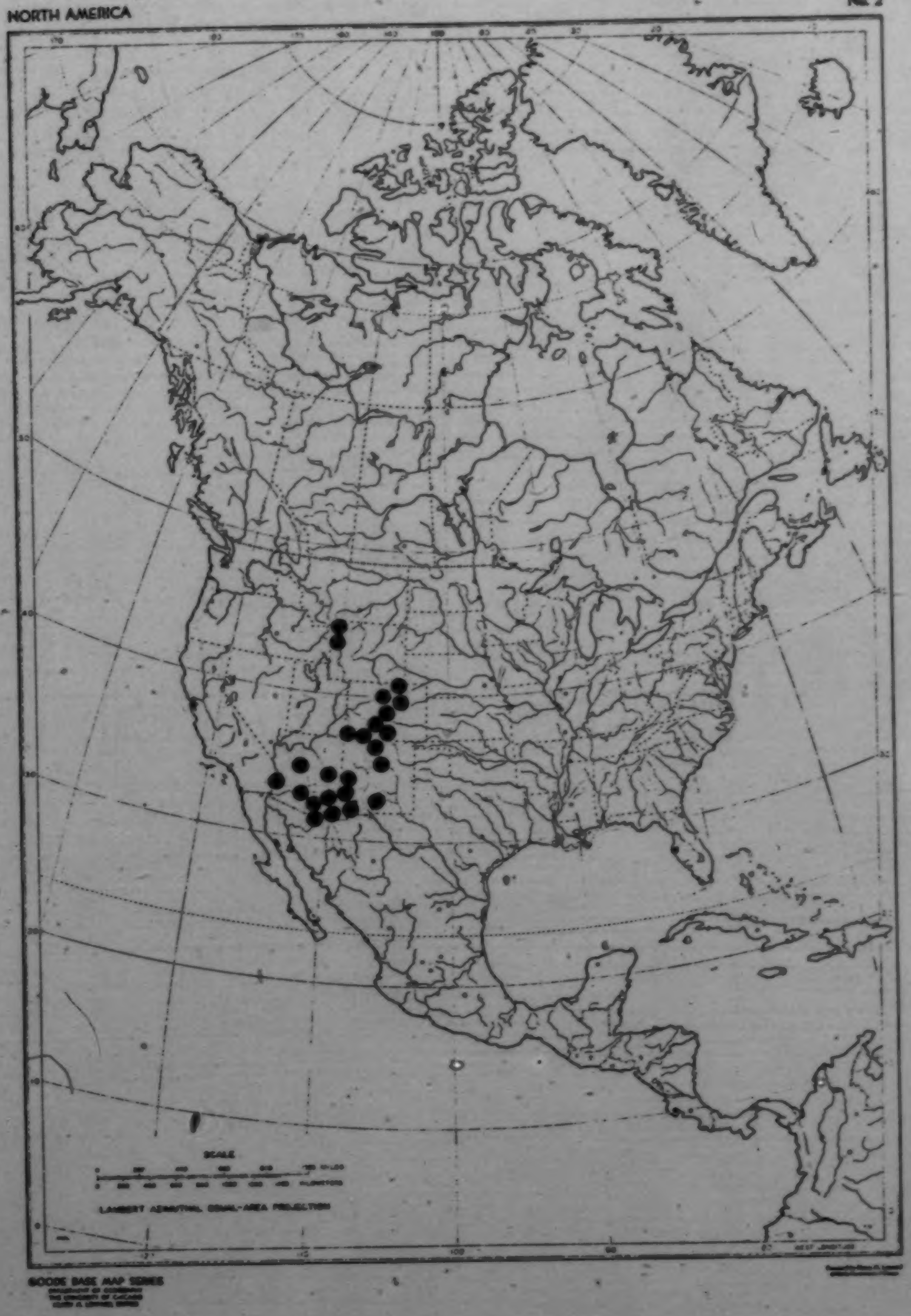
Type: "Orizaba (F. Muller)." not seen. *fide* Williams (1913).

Plants in loose mats, up to 4 cm tall, glossy, light-green, growing on humus or rarely on soil. Stems lightly to moderately tomentose, tomentum white to brown. Leaves when dry straight or slightly falcate-secund, smooth, not undulate, when moist lax, usually spreading, (2.0) 2.5-4.0 (6.5) mm long, lanceolate to broadly lanceolate, tapering to a broadly acute or acute tip, rounded, not keeled or tubulose, both surfaces smooth, margins serrate in upper 1/4, rarely entire, unistratose; costa narrow, 50-75 µm wide just above alar region, subpercurrent or percurrent, slightly toothed on abaxial surface in upper 1/4, costa in median transverse-section showing 4 to 6 guide cells and 2 weak stereid bands, both bands extending into the upper 1/4 of leaf, not to the apex, each band composed of only 1 to 2 rows of moderately developed cells, neither abaxial or adaxial layer of external cells differentiated from stereids; alar cells clear to brown, not extending to costa, unistratose with bistratose regions; basal cells just above alar region rectangular, 40-80 µm long, 12-16 µm wide, thin-walled, slightly pitted; median cells rectangular to linear, 45-70 µm long, 6.0-8.5 µm wide, densely pitted; upper cells long, linear to long-rectangular, 20-30 µm long, 3.0-6.5 µm wide, slightly pitted or smooth. Perichaetial leaves about 2/3 the size of stem leaves, gradually accuminate to a long serrate tip.

Dioicous, male plant as large as or slightly smaller than female. Monosetous, setae yellow to light-brown, 1.5-3.0 cm long. Capsules light-brown, erect to slightly curved, cylindric, 2.0-4.0 mm long, usually strongly ribbed, ribs dark-brown to red, neck short; exothecial cells thick-walled, rectangular; stomates in 1 or 2 loose rows at base of capsule, (27) 32-36 µm; opercula rostrate, 1.5-2.5 mm long; annulus absent; peristome teeth dark-red, vertically striate, 0.3 mm long, 70-85 (100) µm wide at base, divided about half way down and perforate below or sometimes divided completely to base into 2 or 3 irregular segments; spores thin- or thick-walled, papillose, 13-18 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 71): *Dicranum rhabdocarpum* is endemic to North America. It occurs in the Rocky Mountains from northern Wyoming southward into New Mexico and the mountains of central and southern Arizona, and also in the highlands of central Mexico. It is usually found growing on soil or humus in forests or sheltered places, often on north facing slopes (Weber, 1973).

FIGURE 71. The known distribution of *Dicranum rhabdocarpum* Sull.


NORTH AMERICA
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Many specimens have been collected at high elevations, usually between 2100 and 3100 meters in elevation, growing in canyons and other areas where it can find suitable shade and moisture conditions. The species seems well suited to these localities since it is often found in fairly large, lush mats with abundant sporophytes.

Selected Specimens Examined: EXSICCATI. Bartram, Mosses Southern Ariz. 9, as *D. bonjeanii* (FH), 42 (FH). Grout, N. Amer. Musci Perf. 360 (LAF, SMS, CAS, UC, F, DUKE, FH). Clements, Cryptogamae Formationum Coloradensium 196 (UC), 392 (UC). Richards and Drouet, Flora of San Miguel county, New Mexico 479 (UC, F). Holzinger, Musci Acroc. Bor. Amer. 507 (UC, DUKE). Sull. and Lesq., Musci Bor. Amer. (ed. II) 82 (FH).

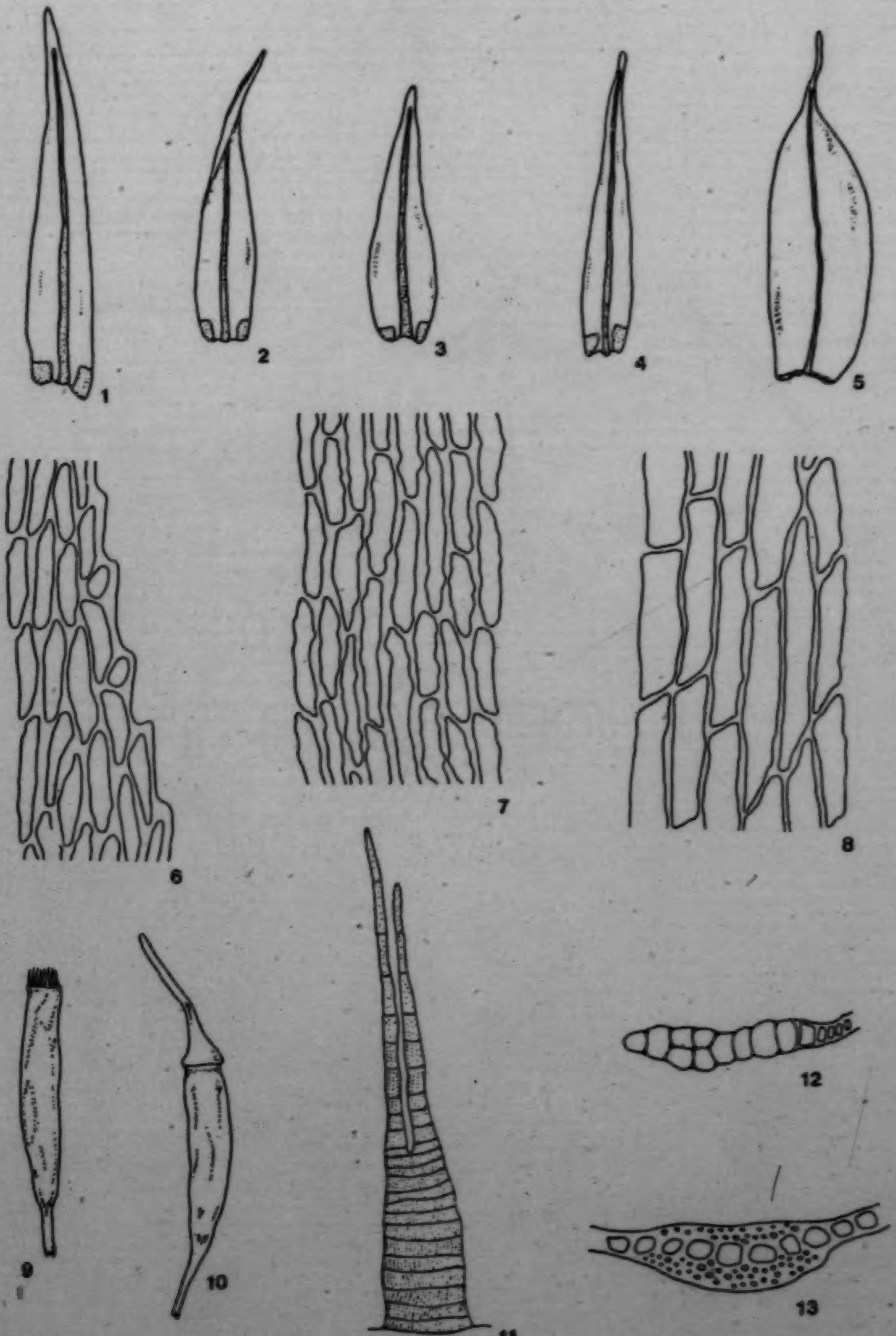
U.S.A. Arizona: Greenlie Co., Hannigan Meadows, Harring 12414 (MNA). Apache Co., Big Lake, Portmann 11416 (ARIZ). Pima Co., Upper Sabino Canyon, Harring 268 (ARIZ). Graham Co., Heliograph Peak, Phillips 2342 (ARIZ). Cochise Co., Rustler's Park, Weber and Shusham 10619 (SMS). Santa Catalina Mtns., Phillips 2350 (COLO). Santa Rita Mtns, Mt. Wright, Haskell and Darrow 3812 (COLO). Colorado: Boulder Co., Peterson 4324 (ALTA). Hinsdale Co., Cebolla Creek Campground, Weber B13060 (LAF). Park Co., Jefferson, Shushan 88 (SMS). Pike's Peak, Eastwood, July 1892 (CAS). Long's Peak, Keiner 360 (UTC). Greenlee Co., McCleary

B1209 (COLO). New Mexico: San Miguel Co., Gallanis River, Richards and Drouet 497 (UC). Grant Co., East Canyon, Holzinger 507 (UC). Santa Fé, Ikenberry 354 (F). Otero Co., Cloudcroft, Whitehouse 129 (COLO). Pecos, Holy Ghost Canyon, Voth V660 (COLO). Taos Co., Carson National Forest, Clebsch B39586 (COLO). Wyoming: Teton Co., Jackson Lake, Redfearn B11352 (MICH). Yellowstone National Park, Sheppard B36148 (COLO).

Dicranum rhabdocarpum is one of the more distinct and easily recognized species in the section *Dicranum*., since it has a combination of morphological characters (long upper cells, ± erect capsules, partially unistratose alar cells) and a narrow, distribution that can be used separate it from other species. Although it is a taxonomically sound species, its systematic position within *Dicranum* is questionable. Based on erect capsules, some authors (Loeske, 1910; Podpera, 1954) have considered it to be a member of *Orthodicranum*. According to the major criteria I am using for delimiting the genus *Orthodicranum*, *D. rhabdocarpum* must remain within the more inclusive genus *Dicranum*. Of the criteria (Table 1), only two are partially met by this species. The capsules are often erect, but many slightly curved ones occur; the alar cells are essentially unistratose but usually bistratose regions are readily found. In addition, the capsules are strongly ribbed, the peristome is wide (about 80 μm), it lacks specialized asexual reproductive structures, and grows on humus or soil. The later

FIGURE 72. *Dicranum rhabdocarpum* Sull.

1-4	Stem leaves (14x)
5	Perichaetial leaf (9x)
6	Upper laminal cells (280x)
7	Median laminal cells (280x)
8	Basal laminal cells (280x)
9, 10	Capsules (10x)
11	Peristome tooth (140x)
12	Transverse-section of alar cells (140x)
13	Basal transverse section (140x)



four are all character states found generally throughout the genus *Dicranum*, and consequently I prefer to consider *D. rhabdocarpum* an intermediate species between the two genera and retain it within *Dicranum*.

Dicranum rhabdocarpum should never be confused with any species of *Orthodicranum*, even in the sterile state. It has long upper cells, broad leaves, and entire leaf tips, in fact, it superfically resembles *Dicranum scoparium* Hedw. and is occasionally confused with it. These two are easily separated when fertile, since *D. scoparium* has strongly curved capsules. When sterile, closer examination is usually required. The most reliable method for distinguishing *D. rhabdocarpum* from *D. scoparium* is the lamellae present on the abaxial costal surface of latter. These lamellae consist of rows of cells extending from the costa in the form of small "wing-like" structures, sometimes 2 or 3 cells high. *D. rhabdocarpum* will often have teeth on the abaxial costal surface; however, they are not "wing-like" nor more than one cell high. A transverse-section through the alar cells would show a definate bistratose region in *D. scoparium* and only bistratose spots in *D. rhabdocarpum*.

25. *Dicranum amanni* Peterson *nom. nov.**

Type: "GraubÜden - Val Fedoz, 2400 m, Amann". (Holotype-Z!) (the same specimen used to typify *D. latifolium* Amann).

Dicranum latifolium Amann, Flore des Mousses de la Suisse, 2: 53. 1912. *hom. illeg. non Dicranum latifolium* Hedw., Spec. Musc. 140. 1801.

Plants in loose mats or tufts, up to 8 cm tall, usually dark-green, growing on soil or humus, often among rocks. Stems lightly tomentose, tomentum brown. Leaves when dry straight, erect and slightly imbricate, when moist straight, erect and spreading to imbricate, occasionally undulate, 4.0-7.5 (9.0) mm long, 1.5-2.5 mm wide, broadly lanceolate to ovate-lanceolate, rounded, not keeled, tapering to a broadly acute, rounded, or cucullate apex, margins entire or serrate in upper 1/3; costa narrow, about 70 μm just above alar region, sub percurrent, smooth or rarely with 2 weak lamellae on the abaxial surface and extending from the leaf tip to about the middle of leaf; costa in median transverse-section showing 5 to 6 guide cells and 2 stereid bands, both bands disappearing in the apex, neither abaxial or adaxial layer of external cells differentiated from stereid cells; alar cells orange to brown, bistratose, thick-walled, slightly pitted, not extending to costa; basal cells above alar region elongate, pitted, 50-60 μm, median cells elongate, thick-walled, pitted, 60-70 μm; upper cells elongate, thick-walled, pitted, 25-40 µm long, 10-15 µm wide. Perichaetial leaves shorter than stem leaves, innermost ones abruptly narrowed to a subulate tip.

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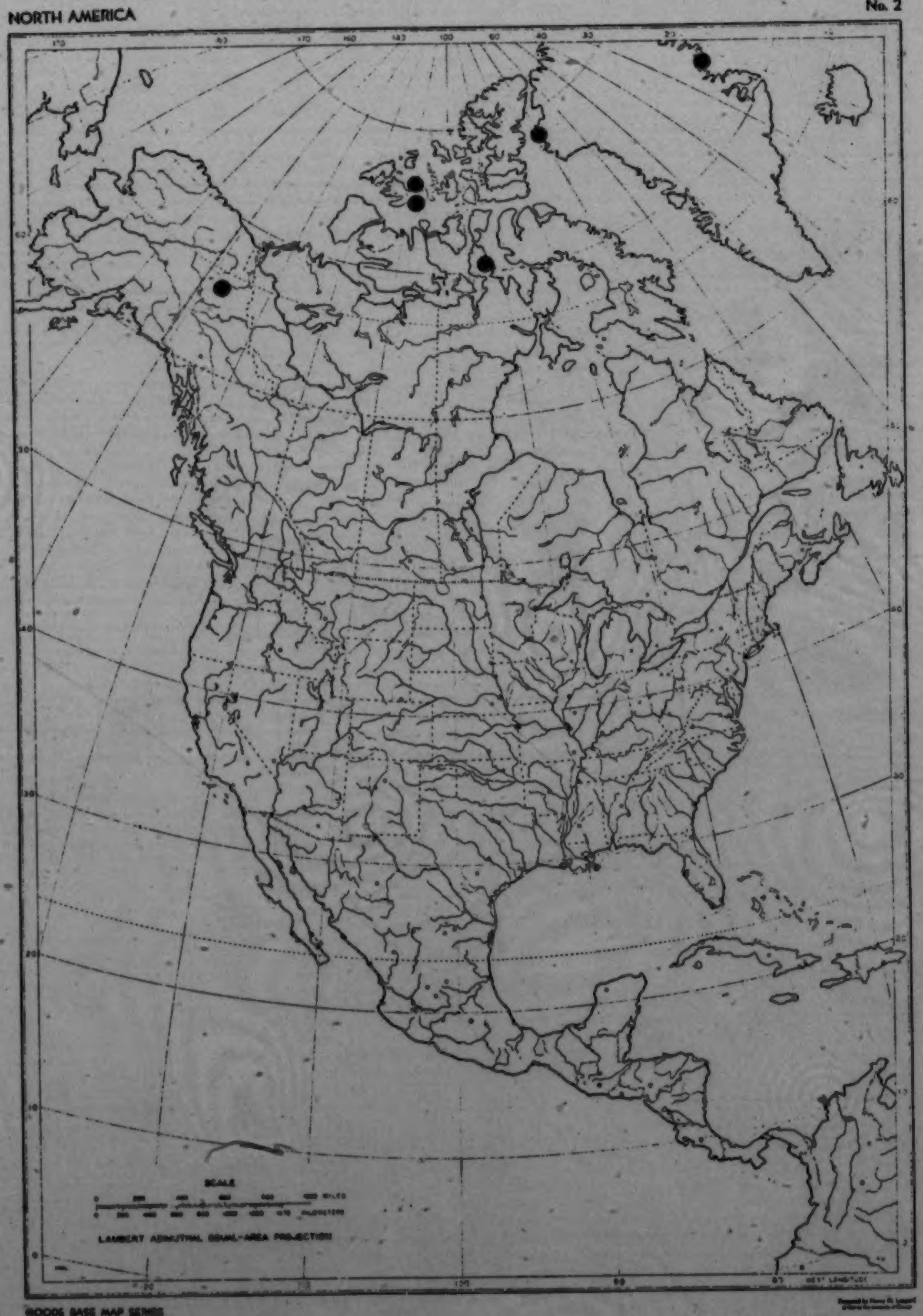
*To be validly published at a later date.

Dioicous, male plants dwarfed and growing on tomentum of female plants. Monosetous, setae light-to dark-brown, 2 to 3 cm long. Capsules brown, 2.0-2.5 mm long, curved, ribbed, not strumose, neck short; exothecial cells short-rectangular, thick-walled, corners often rounded, occasionally pitted, about 70 µm long; stomates in a loose row at base of capsule, 40-45 µm long; opercula rostrate, 1.5 mm long; annulus absent; peristome teeth red, about 0.5 mm long, 80-100 µm wide at base, divided 1/2 to 2/3 way down into 2 segments, vertical striations weak; spores finely papillose, 16-20 µm. Chromosome number unknown.

Habitat and Distribution (Fig. 73): *Dicranum amannii* is not a commonly collected species and very little is known about its ecology. It appears to grown in rocky areas or open tundra in the Arctic and it is apparently restricted to this region in North America. It has been found in Switzerland and Poland in alpine habitats, but as yet hasn't been reported from this type of locality in North America.

Selected Specimens Examined: CANADA. Northwest Territories: Melville Island, Sabine Peninsula, 76°04'N, 108°33'W. Madison M1582 (ALTA). Boothia Peninsula, 70°47'N, 94°00'W, Steen S500

FIGURE 73. The North American distribution of *Dicranum amannii* Peterson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(ALTA). Yukon Territory: Northern Ogilvie Mtns., 65°36'N, 139°04'W, Vitt 13250 (ALTA).

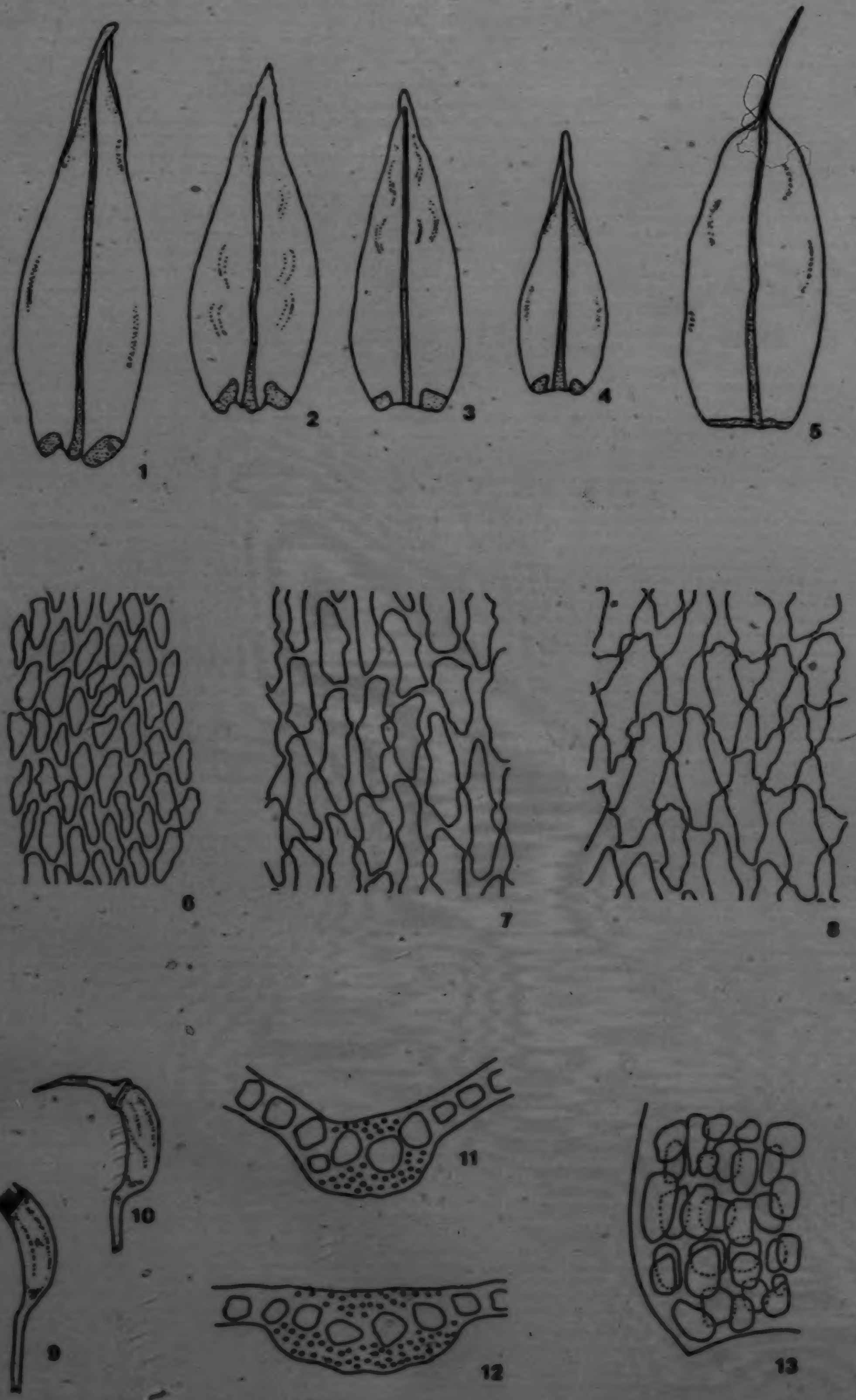
GREENLAND: Parker Snow Bay, Hovey July-Aug., 1916 (NY). Wollaston Foreland, Mt. Zackenberg, 74°28'N, 20°35'W, Holmen July 27, 1950 (CANM).

Taxonomically, *D. amannii* is not difficult to separate from other members of the section *Dicranum*. The broad leaves (Fig. 74-1) with cucullate tips are quite different from any other species of the genus and readily distinguish the species. In addition, the alar cells are very thick-walled and pitted (Fig. 74-13).

Species found in the high Arctic that might be confused with *D. amannii* are *D. angustum*, *D. scoparium*, and *Kiarea glacialis*. All four species are similar in gross appearance and as a result, it is possible that many specimens of *D. amannii* have been passed over by collectors not wanting to take a sample of every *Dicranum* encountered. *Kiaeria glacialis* (not treated) is a species of large size and appearance for *Kiaeria* (most are <2 cm tall) which differs from *Dicranum* by a monoicous sexual state and an internal costal anatomy that lacks well differentiated guide cells and stereid bands. In sterile specimens, which are more common, it is necessary to make a median transverse-section to distinguish it. *Dicranum angustum* is also separable by a median transverse-section

FIGURE 74. *Dicranum amannii* Peterson

1-4 Stem leaves (14x)
5 Perichaetial leaf (9x)
6 Uppers laminal cells (280x)
7 Median laminal cells (280x)
8 Basal laminal cells (280x)
9, 10 Capsules (10x)
11 Median transverse-section (280x)
12 Upper transverse-section (280x)
13 Alar cells (280x)



as it has well developed stereid bands and no lamellae or no remnants of lamellae on the abaxial costa surface. *Dicranum amannii* is distinguishable from *D. scoparium* by the cucullate leaf apex and the thick-walled alar cells of the former. The character states that distinguish these four taxa are summarized in Table 9.

Nomenclature: *Dicranum amannii* was originally described as *D. latifolium* by Amann in 1912. Unfortunately his name choice had previously been used by Hedwig for what is now known as *Desmatodon latifolius* (Hedw.) Brid.; therefore, Amann's name is a later homonym of Hedwig's name and, as such, cannot be used. I have chosen to name this species after Amann since it was his observations and work that resulted in the original description.

TABLE 9. Character states that distinguish three species of *Dicranum* section *Dicranum* and *Kiaeria glacialis*, as they occur in the Arctic.

	D. amannii	*D. angustum*	*D. scoparium*	*K. glacialis*
Leaf Shape	broadly lanceolate to ovate lanceolate	lanceolate	lanceolate to broadly lanceolate	lanceolate to broadly lanceolate
Leaf Tip Shape	cucullate	acute	acute	acute
Alar Cells	thick-walled	thin-walled	thin-walled	thin-walled
Costa Section	5 to 6 guide cells, 2 weak stereid bands	5 to 7 guide cells, 2strong stereid bands	4 to 6 guide cells, 2 weak stereid bands	no distinct guide cells and stereid bands
Lamellae	possibly 2 weak lamellae.	none	possibly 2 to 4 weak lamallae	none

DISCUSSION

Phytogeography

Many studies have been carried out in recent years on North American bryogeography, including such major geographic areas as Canada and the Arctic (Crum, 1966; Persson, 1947, 1952; Schofield, 1972; Steere, 1953, 1965, 1978), northwestern North America (Schofield, 1969; Steere, 1969) eastern North America (Anderson, 1971; Anderson and Zander, 1973; Billings and Anderson, 1966), and the Rocky Mountains (Packer and Vitt, 1974; Weber, 1965). Studies concerning similarities between the North American bryoflora and that of Japan include those of Iwatsuki (1958a, 1972), Iwatsuki and Sharp (1967, 1968), Schofield (1965), and Takaki(1972), while Sharp (1939, 1941, 1966, 1971) and Crum (1951) discuss elements common to the eastern North American bryoflora and that of Mexico and/or Japan. Numerous papers concerning disjunct distribution patterns have been published on such broader distributional problems as bipolar disjuncts (DuRietz, 1940; Sainsbury, 1942; Schofield, 1974; Schuster, 1969), and world-wide disjuncts (Schofield and Crum, 1972).

The bryogeography of numerous genera and species have also been studied (Table 10) and as a result of these studies it has been shown that bryophytes exhibit distribution patterns similar to those of vascular plants (Schofield, 1965) indicating that the factors which have influenced these patterns are the same as those that have influenced the distribution patterns of vascular plants. Long distance dispersal is always a factor to consider in the distribution of bryophytes as the spores are small (usually <30 μm in diameter) and easily transported by the wind. A recent study by van Zanten (1976) using spores from 139 moss species found in New Zealand indicates that one year old spores would germinate in 69% of the species studied if they were not subjected to any freezing or drying; however, when subjected to wet-freezing or dry-freezing conditions of one or four days, the percentage of germinating spores dropped radically. Species that are common to New Zealand and South America had 16% spore germination after 4 days of dry-freezing conditions while under similar conditions, all spores from species known to be common to New Zealand, Australia and Tropical Asia failed to germinate. Van Zanten considered the untreated condition to represent spores dispersed at low altitudes in dry air, while the wet-freezing conditions represent spores dispersed by high altitude air currents. Such data as this support the theory that the long range dispersal is not a major factor in bryogeography even though spores of some weedy species have been germinated after 16 years (Crum, 1972). Obviously, long-distance dispersal cannot be ignored

TABLE 10. Some bryological studies in which distributional information of taxa was presented.

Taxa	Reference
Atrichum	Ireland, 1969a
Bryoxiphium norvegicum	Steere, 1937 Löve and Löve, 1953
Bryum wrightii	Steere and Murray, 1974
Bryobrittonia	Vitt, 1974a Horton, 1978
Calliergon	Karzmarz, 1971
Climacium	Horton and Vitt, 1976
Crumia	Schofield, 1966 Abramova and Dildarin, 1969
Dicranum	Peterson, 1977a, 1977b
Encalypta	Crum, 1963 Horton and Murray, 1976
Fissidens	Iwatsuki, 1958b Steere and Brassard, 1974
Funaria polaris	Steere, 1963
Hygrohypnum	Jamieson, 1976
Oreas martiana	Weber, 1960
Orthotricum	Vitt, 1973
Plagiothecium	Ireland, 1969b
Pseudoscleropdium purum	Lawton, 1960 Dickson, 1967
Rhizomnium	Koponen, 1973
Seligeria	Brassard, 1970 Vitt, 1976
Sphagnum	Andrews, 1938 Maass, 1965, 1966, 1967 Vitt and Andrus, 1975, 1977
Tomenthypnum falcifolium	Vitt and Hamilton, 1975
Voitia	Steere, 1974

entirely as such island floras as that of Hawaii and the Galapagos must have been, at least, partially colonized in this manner (Carlquist, 1974).

If long-distance dispersal is minimal, then other factors must determine the various distribution patterns displayed by moss species. It seems probable that some species are remnants of ancient floras once widespread in temperate regions of Northern Hemisphere and have since been dissected into extant patterns by effects of glaciation, mountain orogeny, peneplanation, continental drift and climatic change. The resultant disjunctions are often more noticeable in bryophytes because they are usually represented by populations of the same species while in vascular plants disjunctions are usually represented by vicarious species or higher taxa (Anderson and Zander, 1973).

Porsild (1958) divided the vascular flora of Canada into six major categories based upon distribution patterns. Subsequent to this, Schofield (1972) published maps of 36 different bryophytes that can be categorized in a similar manner. Anderson and Zander (1973) used 13 categories for the mosses found in the Blue Ridge Province of the Appalachians and Schofield (1969) used over 20 categories and subcategories to classify the distributions of mosses found in northwestern North America. In *Dicranum* and *Orthodicranum*, I have used 8 major categories taken mainly from these three publications. These categories along with the species of *Dicranum* and *Orthodicranum* applicable to each are listed in Table 11.

TABLE 11. The species of the genera *Dicranum* and *Orthodicranum* found in North America, and the basic distribution patterns to which they belong.

Circumboral Pattern	Arctic-Alpine Pattern
Dicranum fragilifolium Brid.	*Dicranum angustum* Lindb.
D. fuscescens Turn.	*D. acutifolium* (Lindb. and Arn.) C. Jens.
D. polysetum Sw.	*D. amannii* Peterson
D. undulatum Brid.	*D. brevifolium* Lindb.
Orthodicranum flagellare (Hedw.) Loeske	*D. elongatum* Schleich.
O. montanum (Hedw.) Loeske	*D. groenlandicum* Brid.
	D. muehlenbeckii B.S.G.
	D. spadiceum Zett.
Amphi-Atlantic Pattern	**Oceanic Pattern**
Dicranum leioneuron Kindb.	*Dicranum majus* Sm.
Eastern North America - Europe	**Western North America - Europe**
Dicranum spurium Hedw.	*Orthodicranum strictum* Culm.
Orthodicranum fulvum (Hooke) Roth.	
O. viride (Sull.) Roth.	

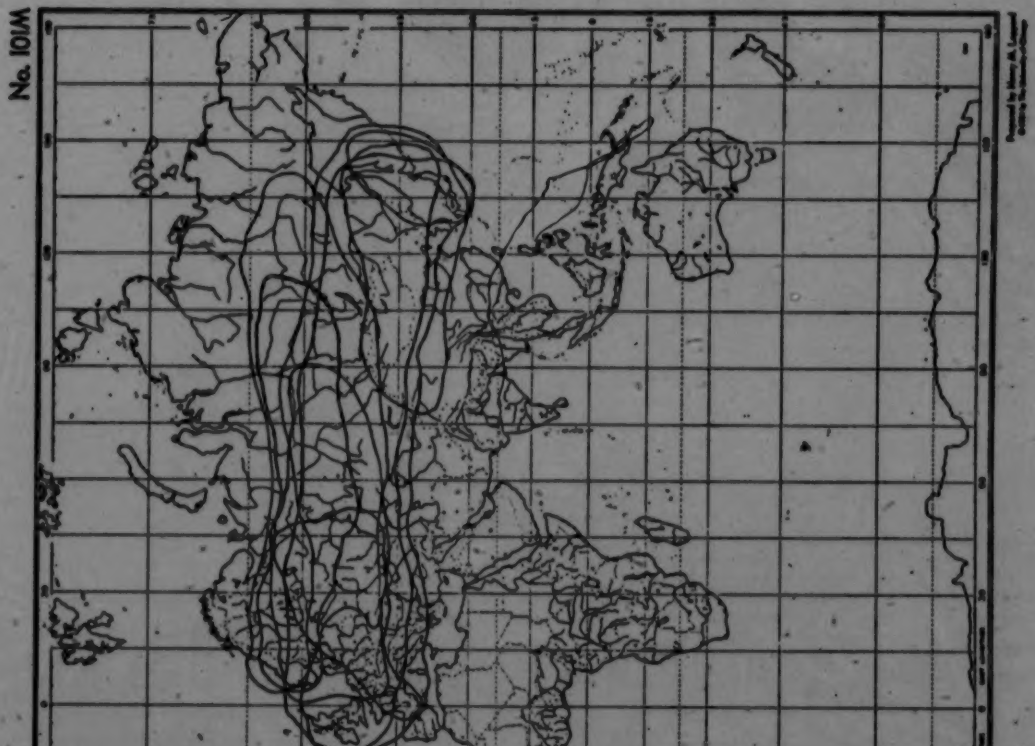
TABLE 11. (Continued)

Circumboreal - Disjunct in New Zealand	North American Endemic
Dicranum scoparium Hedw.	*Dicranum condensatum* Hedw.
	D. ontariense Peterson
	D. pallidisetum (Bailey) Ireland
	D. rhabdocarpum Sull.
	D. sulcatum Kindb.
	D. brevifolium var. *bistratosum* Peterson and Ireland

Circumboreal Species (Fig. 75): Six species of *Dicranum* and *Orthodicranum* are classified in this category. All are generally widely distributed throughout North America, Europe, and Asia, usually between latitudes of about 40^{o}N and 60^{o}N although *O. flagellare* (Fig. 14) and *O. montanum* (Fig. 16) do extend southward into Mexico and the other species are occasionally found near the arctic circle in northern Alaska or the Yukon.

All six species no doubt survived glaciation in suitable areas south of the glacial margin and recolonized the more northern areas after the glacial retreat. Five of the species are associated with forest habitats, *D. fragilifolium* (Fig. 24), *D. fuscescens* (Fig. 26), *O. flagellare* (Fig. 14) and *O. montanum* (Fig. 16) grow on logs while *D. polysetum* (Fig. 60) grows on humus in forests. As a consequence, it would have been relatively easy for them to move southward and then again northward along with their vascular plant hosts. The remaining species, *D. undulatum* (Fig. 56) is a species of mire and fen habitats and probably survived in areas near the glacial margin and gradually recolonized the many suitable localities created and left by the retreating glaciers. This idea is supported by fossil specimens collected from strata deposited during the interm between the Nebraskian and Kansasian glacial advanced in Iowa (Miller, 1976). It is also possible that some of these species could have survived glaciation in Beringia, the unglaciated area of Alaska and the Yukon Territory, and recolonized the area now occupied by radiating from there in a manner similar to that proposed by Hultén (1937).

FIGURE 75. Circumboreal distribution pattern showing the overlapping ranges of six *Dicranum* and *Orthodicranum* species as they are known to occur in North America and Eurasia.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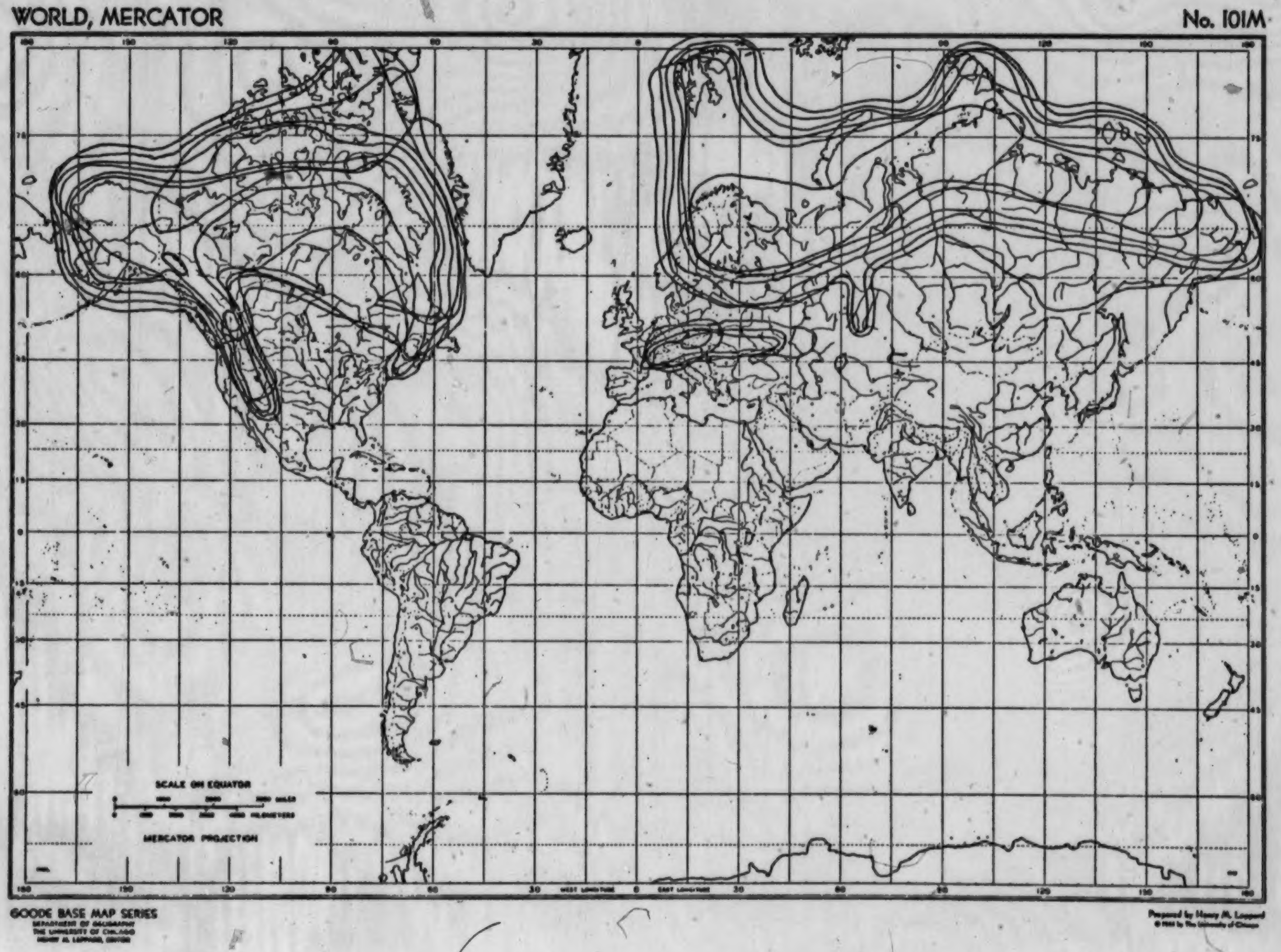
Survival in Beringia could explain the isolated populations of *O. montanum* found in Alaska.

Other bryophytes with similar distribution patterns to these six species include; the hepatics *Ptilidium ciliare* (L.) Hampe, *Barbilophozia lycopioides* (Wallr.) Loeske, *Mylia anomala* (Hook.) S. Gray, *Conocephalum conicum* (L.) Lindb.; the mosses *Distichium capillaceum* (Hedw.) B.S.G., *Tetraphis pellucida* Hedw., *Pleurozium schreberi* (Brid.) Mitt., and *Sphagnum fuscum* (Schimp.) Klinggr. (Schofield, 1969). Some vascular plants with similar patterns are *Galium boreale* L., *Potamogeton natans* L., *Potentilla palustris* (L.) Scop., *Epilobium angustifolium* L., (Hultén, 1968). It should also be noted that although such major forest trees as *Populus tremuloides* Michx. and *Picea glauca* (Moench.) Voss do not occur across the boreal region of Europe and Asia, such closely related species as *Populus tremula* L. and *Picea abies* Karsten do occur and probably perform similar roles in providing substrates for these mosses.

Arctic-Alpine Species (Fig. 76): Eight species of Dicrana are included in this category. In general, the species occur, in North America, from the Canadian Arctic Archipelago and northern Alaska southward as far as 55°N. In the Rocky Mountains some are found in suitable habitats as far south as northern New Mexico and in the east, they may be found in similar areas southward to the mountains of New Hampshire and Vermont. For the most part, their southern

FIGURE 76. Arctic-Alpine distribution pattern showing the overlapping ranges of nine *Dicranum* taxa as they are known to occur in North America and Eurasia.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SCALE ON EQUATOR
0 1000 2000 3000 MILES
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MERCATOR PROJECTION
WEST LONGITUDE
EAST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard
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limit of distribution in the north closely follows the southern limit of tundra (Rowe, 1972) although *D. acutifolium* (Fig. 52) does commonly extend into the boreal forest.

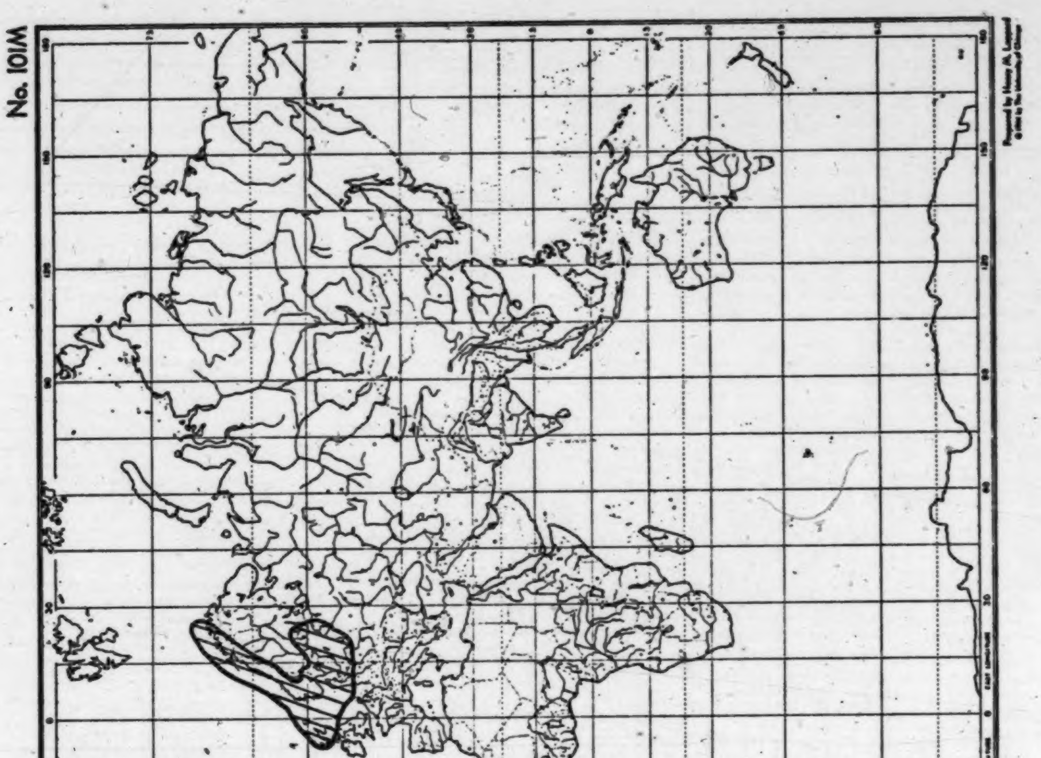
The eight species in this category can be divided into 3 sub-groups. Six of the species in Table 10 are true arctic-alpine species; however, the other two are not. Both varieties of *D. brevifolium* (Figs. 38, 40) are apparently circumalpine in distribution. *Dicranum amannii* (Fig. 73) is quite similar to Porsild's "Arctic Archipelago endemic element" (Porsild, 1958); however, it differs since it is also found in the alps of Switzerland. A point of note is that at present *D. amannii* has only been collected on paleozoic substrate composed mostly of shales and carbonates (Porsild, 1958) and may be specific to such substrates. If such a correlation exists, the scarcity of *D. amannii* collections is understood as this substrate is limited in the Arctic.

The present distribution pattern of these species suggests that for the most part, they survived glaciation in Beringia and other such refugia as Banks Island, Northwest Greenland (Gelting, 1934), and possibly some areas in the Rocky Mountains (Packer and Vitt, 1974). This being the case, the species radiated from Beringia and the other refugia after glaciation in a pattern similar to Hultén's (1937) plate 29 (he referred to these plants as Arctic-Montane species). Apparently these species are found in the alpine regions not only by radiating from Beringia, but because they managed to survive glaciation in smaller refugia (nunatacs) and later disperse from them. It is also possible they were distributed in alpine habitats before glaciation and survived both north and south of the ice.

Other bryophytes with similar distribution patterns include; the hepatics *Cephaloziella arctica* Bryhn et Douin, *Lophozia alpestris* (Schleich. *ex* Web.) Evans, *Tritomaria exsecta* (Schrad.) Loeske, *Scapania subalpina* (Nees) Dum., *Pleurocladia albescens* (Hook.) Spruce; the mosses *Stegonia latifolia* (Schwaegr. *ex* Schultes) Vent. *ex* Broth., *Aulacomnium acuminatum* (Lindb. and Arn.) Par., *Cirriphyllum cirrosum* (Schwegr. *ex* Schultes) Grout, and *Hypnum bambergeri* Schimp. (Schofield, 1969). Vascular plants with similar distribution patterns include *Lycopodium alpinum* L., *Kobresia myosuroides* (Vill.) Fiori and Paol., *Carex misandra* R. Br., *Silene acaulis* L., *Saxifraga oppositifolia* L., and *Achillea borealis* Bong. (Hultén, 1968).

Amphi-Atlantic Pattern (Fig. 77): One species, *D. leioneuron* (Fig. 69) has this type of distribution. It is found in the Maritime Provinces of Canada, and in Scotland and Scandinavia, where it grows only in ombrotrophic bogs. The distribution pattern is similar to that of *Sphagnum angermanicum* Melin, as shown by Maass (1966), and only slightly different from other such species as *Hypnum imponens* (Hedw.) P. Beauv., (Schofield, 1972), and *Orthotrichum gymnostomium* Bruch *ex* Brid. (Vitt, 1973).

FIGURE 77. Amphi-Atlantic distribution pattern showing the range of *Dicranum leioneuron* Kindb. as it is known to occur in North America and Europe.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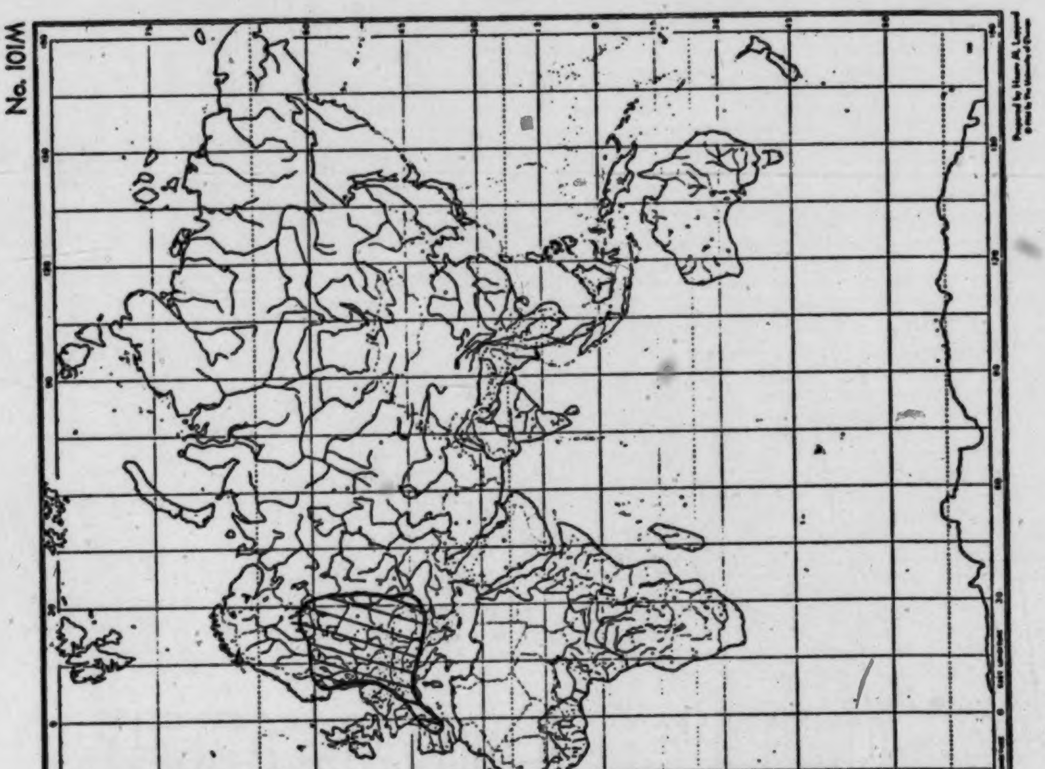
This distribution pattern is difficult to explain in that the area in Canada where the species is now found was glaciated (Prest, 1969). Refugial areas have been proposed for the Gaspé region (Fernald, 1925) and Ellesmere Island (Schuster, 1959); however, *D. leioneuron* has not been found in either of these two areas. It is possible that long distance dispersal is responsible for this pattern. Størmer (1969) provided information indicating *Orthodontium lineare* was introduced to Holland from Great Britian by long distance spore dispersal and Vitt (1973) suggested *Orthotrichum gymnostomum* was introduced to North America by horticultural introduction. Similiarly, *D. leioneuron* could have arrived in North America after glaciation via long distance spore dispersal or by introduction. Another explanation is that 65 million years ago, when the North American and European continents were connected (Dietz and Holden, 1970), the distribution was continuous, explaining the presence of the species on both sides of the Atlantic ocean. One can hence assume that the species survived glaciation by migrating southward along the front of the glaciers, possibly surviving on the continental shelf. After glacial retreat, this species could have migrated northward to its present localities.

Western North-America-Europe Disjuncts (Fig. 78): One species of the genus *Orthodicranum* falls into this category. *Orthodicranum strictum* (Fig. 22) is confined to the west coast of North America, ranging from southern Alaska to central California while also

FIGURE 78. Western North American-Europe disjunct pattern showing the range of *Orthodicranum strictum* Culm.as it is known to occur in North America and Europe.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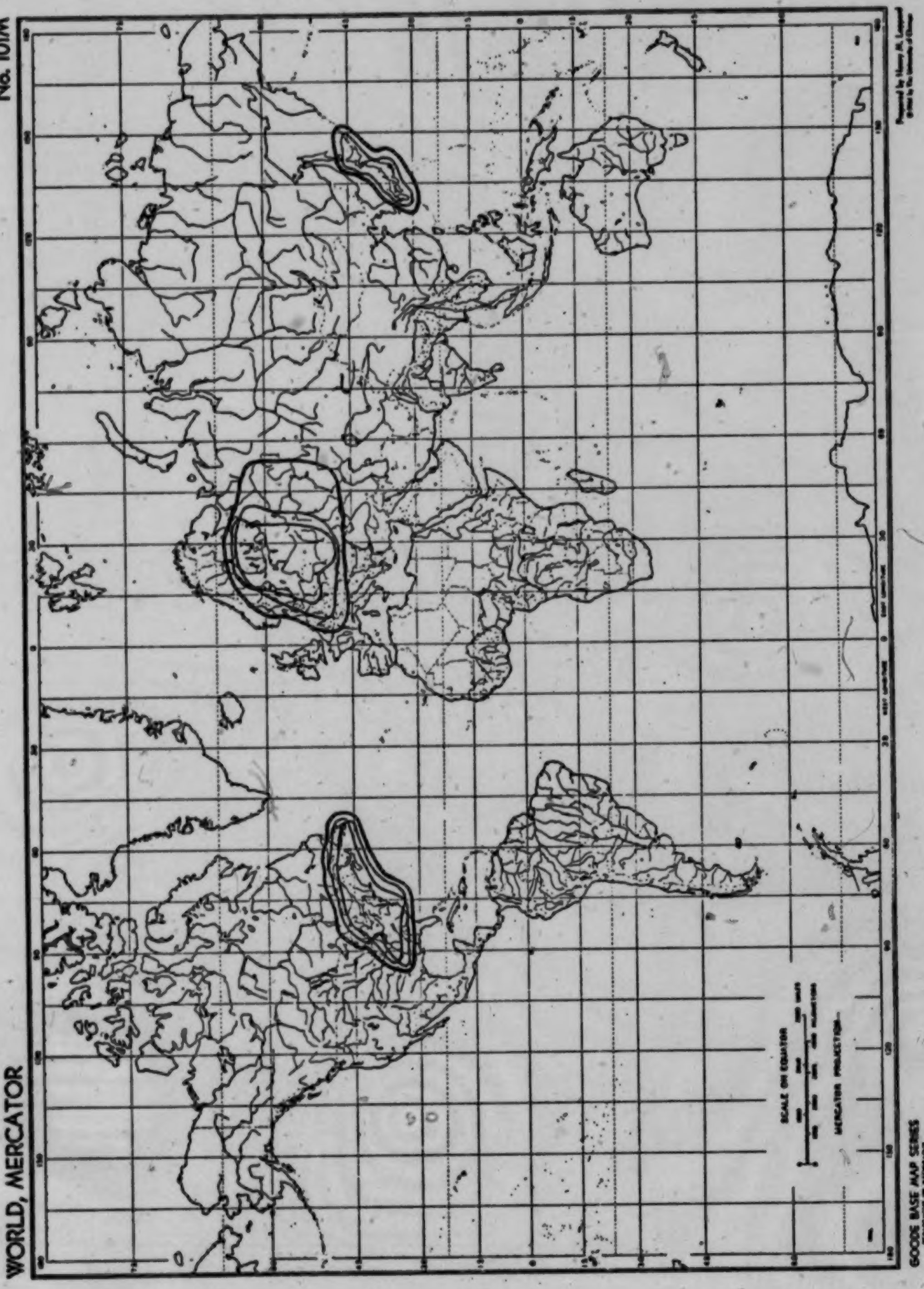
occurring in central Europe and Scandinavia. The species is probably a remnant of a once widespread or circumboreal flora such as one of Tertiary times (Schofield, 1969) and, like *Sequoia sempervirens* (one of its hosts), survived glaciation and various orogenic activity in isolated localities. No doubt it survived glaciation along with these trees and later spread northward into favourable habitats among *Picea sitchensis* (Bong.) Carr. and *Thuja* species.

Other species that have this type of distribution are the hepatics *Mastigophora woodsii* (Hook.) Nees, *Plagiochila asplenioides* Schust., *Marsupella alpina* (Berggr.) Bryhn *et* Kaal., *Porella cordaeana* Hüb. Moore, and *Moerckia blyttii* (Moerck.) Brockm. The mosses include *Andreaea nivalis* Hook., *Barbula vinealis* Brid., *Tortula princeps* De Not., *Hookera lucens* (Hedw.) Sm., and *Plagiothecium undulatum* (Hedw.) B.S.G. Vascular plants with a similar pattern include *Equisetum telmateia* Ehrh., *Blechnum spicant* (L.) Roth., *Thelypteris oreopteris* (Ehrh.) Slosson, and *Carex stenophylla* Wahlenb. (Schofield, 1969).

Eastern North American-Europe Disjuncts (Fig. 79): This pattern is represented by *Dicranum spurium* (Fig. 50), *Orthodicranum fulvum* (Fig. 18), and *O. viride* (Fig. 20). In North America, all three species have a very similar range, being found as far south as northern Georgia, and north-eastern Texas, and extending northward to Minnesota and Newfoundland. The southern limit corresponds closely to the boundaries of the Oak-Hickory-Pine forest, while

FIGURE 79. Eastern North America-Europe disjunct pattern showing the overlapping ranges of *Dicranum spurium* Hedw. and two *Orthodicranum* species as they are known to occur in North America and Europe. The occurrence of *O. fulvum* and a variety of *O. viride* in Japan is also indicated.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SCALE ON EQUATOR
MERCATOR PROJECTION
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a similar Oak-Hickory forest forms the western boundary (Braun, 1950). The northern boundary of this distribution pattern is similar to the northern limits of the northern Hardwood forest as well as being just north of the southern extent of glaciation. In Europe, *O. fulvum* and *O. viride* seem to have a distribution confined to the area between the Pyrenees, the Alps, and central Scandinavia (Takaki, 1972) while *D. spurium* is more widespread, even occurring in western Russia (Podpera, 1954). In addition, *O. fulvum* and a variety of *O. viride* are reported from Japan (Takaki, 1972).

The origin of the moss flora in eastern North America is discussed by Anderson (1971), Anderson and Zander (1973), and especially by Crum (1972), and many comparisons have been made concerning similarities between the bryoflora of this region and that of Japan (Iwatsuki, 1958; Iwatsuki and Sharp, 1967, 1968; Sharp and Iwatsuki, 1965); however, there seem to be few reports of species with distributions similar to that of these three species. It is the conclusion of most bryologists that a large portion of the flora in eastern North America is an Arctotertiary remnant, and that species have survived in this area probably in the Appalachian, the Ozark, and the Ouchita Mountains, while the surrounding flora was eliminated. Glaciation and other such phenonema as the elevation of the Rocky Mountains (resulting in a dryer interior climate), and peneplanation cycles were major forces in the elimination process (Crum, 1972).

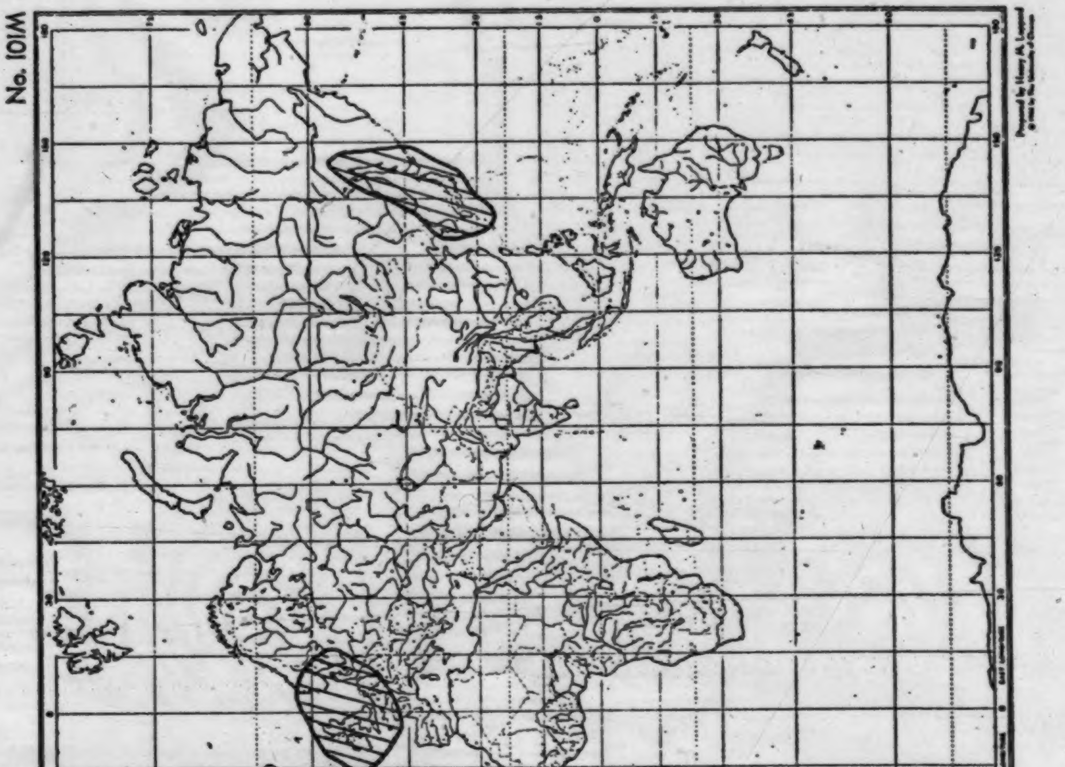
Dicranum spurium, *O. fulvum*, and *O. viride* should be considered members of this flora, and therefore, they were probably distributed in a circumboreal pattern in the Tertiary. Now they occur only in areas where remnants of this flora remain, or in areas to which they might easily migrate.

Other species with a eastern North-America-Europe pattern are *Isothecium eumyosuroides* Dix. and *Hygrohypnum novae-caesarae* (Aust.) Grout, although they do differ from the pattern shown by the species in this treatment, being confined to the Appalachian Mountains of North America. *Anomodon rugellii* (C.Müll.) Keissl., *Thamnobryum alleghaniense* (C.Müll.) Nieul., *Rhabdoweisia crenulata* (Mitt.) Jameson, and *Brachydon trichoides* (Web.) Nees, Hornsch. and Sturm are four species that occur in the Appalachians, Europe, and eastern Asia, not unlike the pattern shown by *O. fulvum*, *O. viride*, and the Japanese variety of *O. viride*.

This distribution pattern is represented in the vascular flora by such North America-Europe vicariants as *Juniperus virginiana* L.-*J. sabina* L.; *Oxalis montana* Raf.- *O. acetosella* L.; and *Scrophularia marilandica* L.- *S. nodosa* L. (Cain, 1944).

Oceanic Disjunct Pattern (Fig. 80): *Dicranum majus* (Fig. 62) occurs on both coasts of North America, as well as in coastal Europe and Japan. Essentially it is both amphiatlantic and amphipacific in distribution, and restricted to suboceanic conditions. It does not

FIGURE 80. Oceanic distribution pattern showing the range of *Dicranum majus* Sm. as it is known to occur in North America, Europe, and Asia.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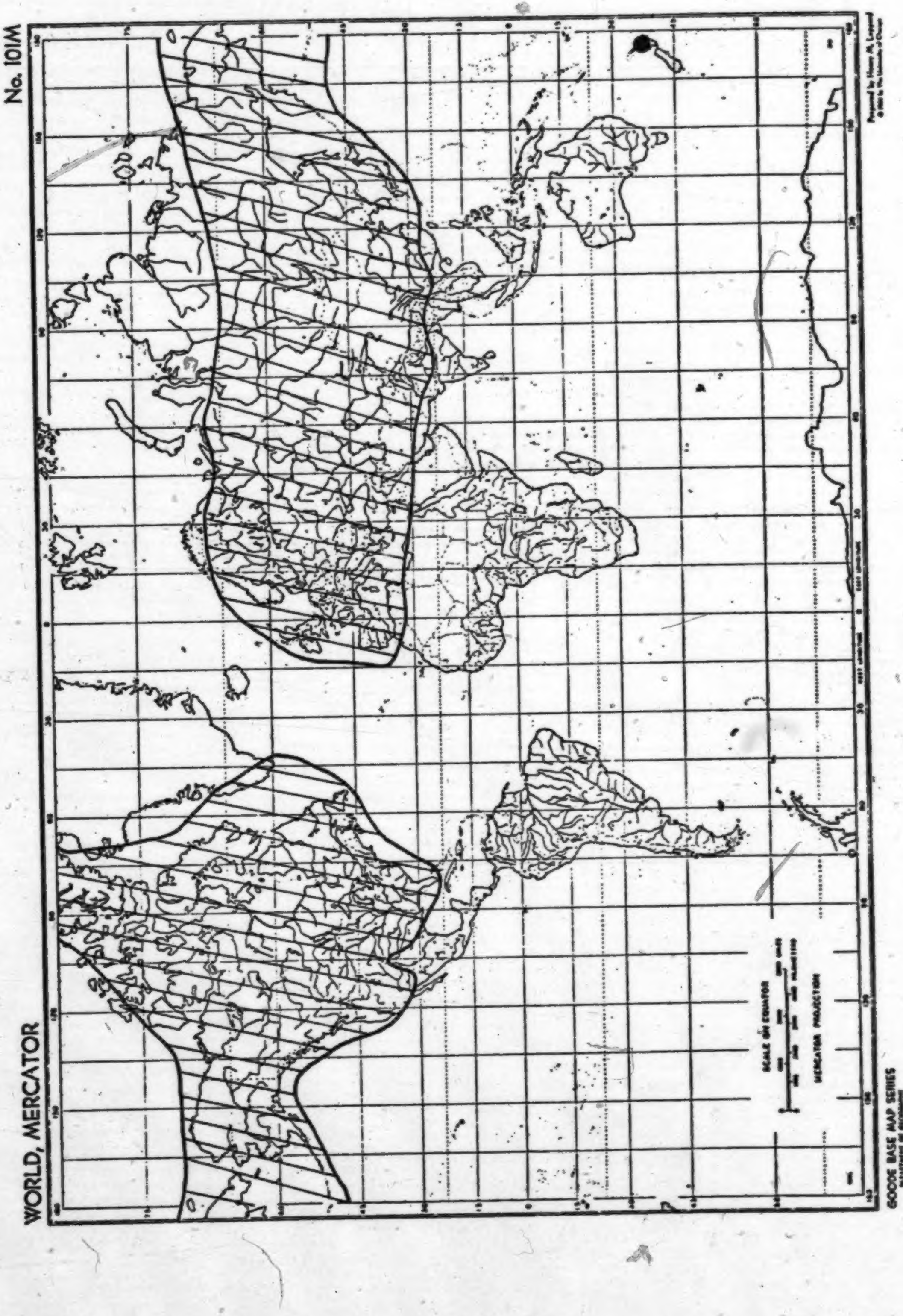
grow in salt spray; however, it may be collected quite near the shore in mesophytic forests, usually growing on humus.

It might be argued that this distribution pattern is a result of long distance dispersal, at least as far as the disjunctions between eastern and western North America are concerned. This could be suppported by the occasional site in the interior (Alberta, Great Bear Lake); however, there are many other seemingly suitable habitats between the two coasts that do not contain *D. majus*. In my opinion, a more acceptable theory is that *D. majus* is a remnant of a flora that ranged from coast to coast, or possibly even circumboreal, in times prior to the orogeny of the western cordilleran. If this is the case, the connection between the two coasts are explained. From that point the species probably survived glaciation south of the glacial margin and migrated northward on each coast after the glacial retreat. The sites in Japan are explanable by similar survival or by migration around the northern perimeter of the Pacific via the Aleutian Islands (Schofield, 1969). The European populations are most easily explained by survival in areas south of glaciation boundaries.

There seem to be few species that extend both around the northern perimeter of the Atlantic Ocean and around the northern perimeter of the Pacific while not occurring across either continental North America or continental Eurasia. Those species that do have this distribution pattern are found in marshes, bogs, streams and woods near the ocean and at least one, *Grimmia maritima* occurs on rocks in intertidal areas. Two other mosses that closely parallel this distribution pattern are *Pohlia annotina* Hedw. and *Ulota hutchinsiae* (Sm.) Hamm. Vascular plants include *Zostera marina* L., *Eriophorum russeolum* E. Fries, *Montia fontana* L., *Lathyrus maritimus* L., and *Cornus suecica* L.(Hultén, 1968).

Circumboreal-Disjunct in New Zealand (Fig. 81): *Dicranum scoparium* (Fig. 64), the most widespread member of the genus, occurs throughout the temperate regions of North America, Europe, and Asia and may occasionally be collected in more northern areas. It is also disjunct in New Zealand. Patterns similar to this have been explained by transtropical mountain chains (Du Rietz, 1940); however, the species has not been found in intermediate areas. A second theory might be continental drift. If so, *D. scoparium* must be a very ancient species having existed in the Cretaceous period when Australia was still a part of Gondwanaland (Dietz and Holden, 1970). I find this theory hard to accept since there is no morphological difference between specimens collected in New Zealand and North America. It is generally accepted that mosses are an ancient group that evolve slowly; however, it does not seem likely that no difference, in such disjunct popultions, would be found after more than 100 million years. Other possible explanations for this pattern include long distance dispersal, and human introduction. If human introduction, by means of contaminated horticultural specimens

FIGURE 81. Circumboreal-disjunct in New Zealand pattern showing the range of *Dicranum scoparium* Hedw. as it is known to occur in the world.


WORLD, MERCATOR
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SCALE ON EQUATOR
MERCATOR PROJECTION
GOODE BASE MAP SERIES

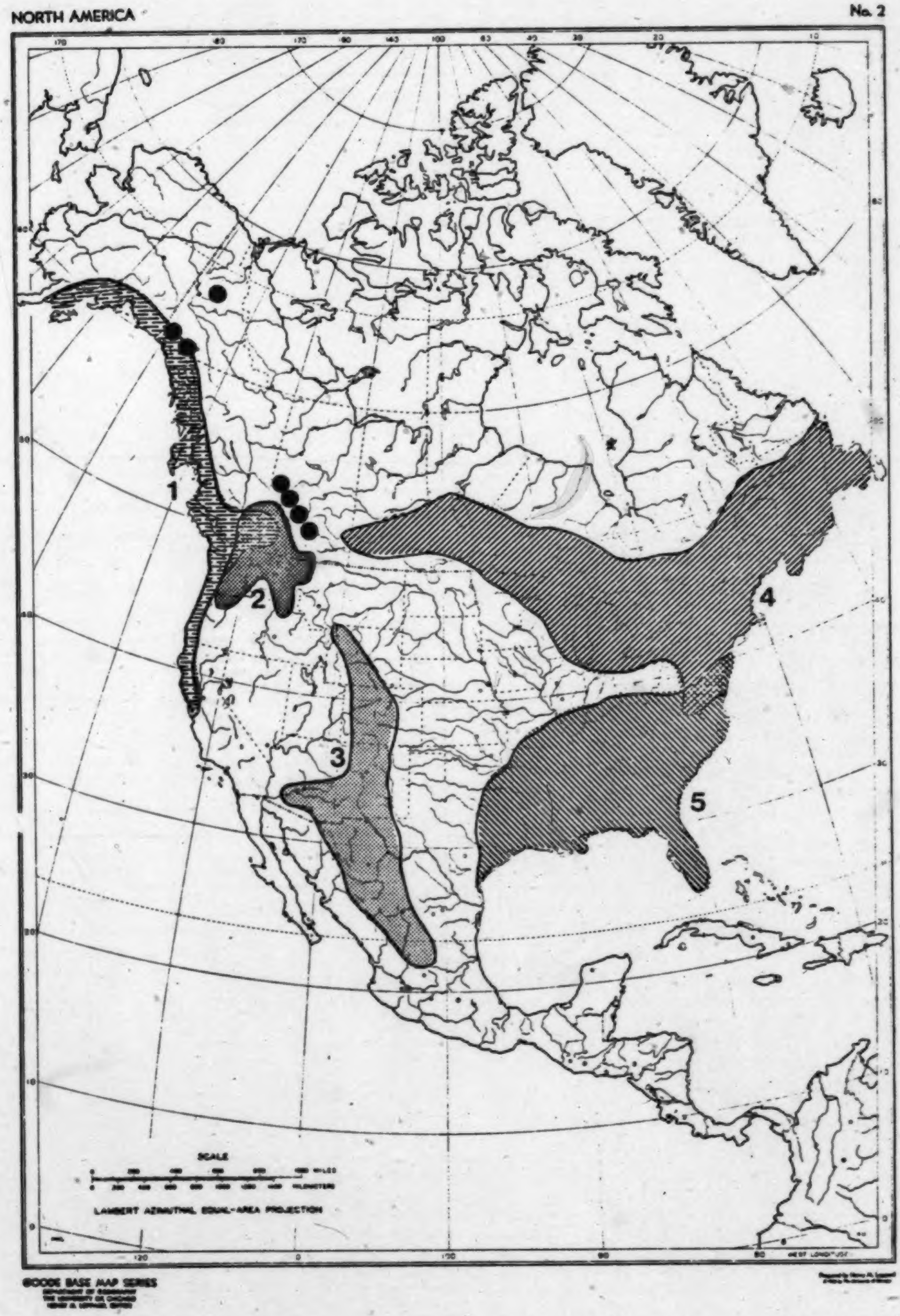
or livestock, was the answer specimens would be expected in urban areas instead of the more remote localities in which they have actually been found. Long distance dispersal, like the trans-tropical mountain theory should result in populations occurring in intermediate areas. Although this is not the case for *D. scoparium* and a number of other species, there are others that have disjunct distributions similar to that *D. scoparium* including scattered intermediate localities (Schofield, 1974) and, as a result, long distance dispersal seems to be the most plausable answer. Also, the specimens of *D. scoparium* are sterile and known from only three localities. According to Schofield (1974) this could support the long distance dispersal theory since *D. scoparium* is dioicous and the probability of a single spore falling in an area is obviously greater than two spores falling in the same spot. If fertile specimens are found in New Zealand then one of the other theories would rate consideration.

Other mosses that have a similar distribution to that of *D. scoparium* are *Tortella fragilis* (Hook. and Wils.), *Brachythecium velutinum* (Hedw.) B.S.G. (Vitt, 1974), *Climacium dendroides* (Hedw.) Web. and Mohr (Horton and Vitt, 1976), *Hylocomnium splendens* (Hedw.) B.S.G. (Schofield and Crum, 1972), *Fissidens adianthoides* Hedw., *Ditrichum flexicaule* (Schwaeger.) Hampe, *Tortula laevipila* (Brid.) Schwaegr., *Grimmia trichophylla* Grev., *Funaria microstoma* B.S.G., *Isopterygium pulchellum* (Hedw.) Jaeg. and Sauerb., (Sainsbury, 1942. 1955), *Pleurozium schreberi* (Brid.) Mitt. (Schofield, 1969), and *Orthotrichum alpestre* Hornsch. *ex* B.S.G. (Vitt, 1973). Such vascular plants as *Potamogeton filiformis* Pers., *Triglochin palustre* L., *Chenopodium glaucum* L., and *Hieracium gracile* Hook. have distributions similar to these mosses (Schofield, 1969) even though they do seem to be poor examples for long distance dispersal.

North American Endemics (Fig. 82): Five species and one variety of *Dicranum* are endemic to North America. All are found in separate geographic areas and probably evolved autochthonously from widespread relatives. The various such phenomena of the past as orogeny of the western cordilleron and the subsequent drying of the interior, glacial advance and retreat, and the resultant lowering of the ocean levels undoubtly created a number of new habitats as well as dismembered the extant flora.

Two species, *D. pallidisetum* (Fig. 31) and *D. sulcatum* (Fig. 28) are apparently derived from the circumboreal *D. fuscescens* (Fig. 26) and occupy limited ranges along coastal British Columbia, Washington, Oregon, and California (*D. sulcatum*) and in the interior subalpine areas of Washington, Idaho, and British Columbia (*D. pallidisetum*). *Dicranum fuscescens* was probably a widespread species occurring across the North American Continent before the orogeny of the western cordilleron and, when orogeny occurred, was separated into two or more isolated areas. The mountains would have provided sufficient geographic isolation for speciation of both *D. sulcatum* and *D. pallidisetum* to occur. Each species has evolved into a

FIGURE 82. The approximate geographical ranges of the taxa of *Dicranum* Hedw. which are endemic to North America. No. 1 is *D. sulcatum*, No. 2 is *D. pallidisetum*, No. 3 is *D. rhabdocarpum*, No. 4 is *D. ontariense*, No. 5 is *D. condensatum*, the dots represent known localities of *D. brevifolium* var. *bistratosum*.


NORTH AMERICA
No. 2
1
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SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES

habitat not normally occupied by *D. fuscescens*. *Dicranum sulcatum* occurs primarily on living coniferous trees in the coastal forest while *D. pallidisetum* occurs on humus or soil in subalpine communities. *Dicranum fuscescens* occurs on logs and stumps, usually of angiospermous trees. As a result of their special habitat requirements, the new species have been able to maintain ecological isolation from *D. fuscescens* even though they are now sympatric with it. The present sympatric condition probably resulted from recolonization of the widespread *D. fuscescens* during more recent times.

Dicranum rhabdocarpum (Fig. 71) also seems to have evolved after the orogeny of the Rocky Mountains. Of the other species in North America, *D. rhabdocarpum* is apparently most closely related to the circumboreal *D. scoparium* (Fig. 65). It is probable that a population of *D. scoparium* was isolated in the mountainous regions and while both groups evolved over time, the mutations occurring in the smaller population of the mountains would be maintained by the small gene pool while those occurring in the still widespread population would be buffered by the larger gene pool. At present, both species are found over the same geographic range, with *D. rhabdocarpum* occurring only in the Rocky Mountains and apparently lacking the genetic adaptability to colonize other areas. As both species occur in the same area with little ecological separation, it is probable that reproductive isolation exists.

Dicranum condensatum (Fig. 47) and *D. ontariense* (Fig. 54) are members of section *Spuria* and found in eastern North America and both probably evolved in association with glacial events. The section *Spuria* contains five species in North America; the most widespread species, *D. undulatum* grows in mires and fens throughout the boreal region; *D. spurium* grows in temperate forests of eastern North America and Europe; *D. acutifolium* (Fig. 52) grows in tundra and forests of the arctic and alpine regions; *D. ontariense* is confined to the St. Lawrence River area, and *D. condensatum* is found primarily in the southeastern portion of the United States (growing on sandy soil).

By speculation of the section *Spuria*, one could suggest the following events: During Tertiary times there were two species in section *Spuria* occurring in North America; *Dicranum undulatum* (or something very similar to it) occurring in wetland habitats of the boreal region, and *D. spurium* found in the drier forest habitats. As the glaciers advanced, *D. undulatum* probably migrated southward along the margin of the glacier. In addition, a population of this species would have been isolated in Beringia. Both populations would have evolved at different rates under different selective pressures with the Beringia survivor radiating outward during postglacial or interglacial times as the extant *D. acutifolium*.

In addition, the formation of the glaciers also caused the levels of the oceans to drop, thereby exposing large areas of land. This new habitat provided opportunity for adaptive radiation and both original species gave rise to new taxa: *D. ontariense* from *D. undulatum*, and *D. condensatum* from *D. spurium*. *Dicranum condensatum* probably evolved to occupy the exposed sandy soil while *D. ontariense* is the result of adaptation to the forest habitat from the mires or fen habitat. Since *D. condensatum* now occurs inland one could suggest the species evolved in these areas by ecological isolation. Although this point should be considered, it seems more plausible that the species evolved on the coastal plain where sandy soil was extremely common and migrated inland during more recent times.

The remaining taxon, *D. brevifolium* var. *bistratosum* (Fig. 40) is endemic to subalpine regions of the Canadian Rocky Mountains in Alberta, and the Kluane Mountains and Wernecke Mountains of the Yukon. At this time these populations are considered disjunct although further work may prove the distribution to be continuous. As all sites are north of the maximum extent of glaciation (Prest, 1969) it must be concluded that the taxon either survived glaciation in refugia, or evolved since glaciation. If the distrubution is, in fact, disjunct, the species probably evolved before the last glacial advance and spread along the mountains in a continuous pattern that was later dismembered by the glaciers.

Phylogenetic and Phenetic Relationships in *Dicranum* and *Orthodicranum*

Recent studies of evolutionary relationships within bryophyte genera or families have been few. Examples include works on the Mniaceae (Koponen, 1968a), *Orthotrichum* (Vitt, 1971), *Aloina*, *Aloinella*, and *Crossidium* (Delgadillo, 1975), and *Selgeria* (Vitt, 1976). All have attempted to analysize phylogenetic relationships within a particular group and form a "natural" classification. Lewinsky (1977) provided a phylogenetic diagram of *Orthotrichum*; however, she did not provide a character analysis. Other studies on the Sematophyllaceae (Seki, 1968) and *Acrolejeunea* (Gradstein, 1975) have been conducted in a phenetic manner. Hypothetical "trees" may be constructed from phenetic investigations, but such processes as convergent and parallel evolution are not concidered.

In attempting a phylogenetic study, it is necessary to establish the nature of various character states in order to position the taxa in a phylogenetic manner. Methods for arranging the taxa into a phylogenetic scheme have been established by Henning (1950, 1965, 1966) in what is termed the "sister group" approach, and by Wagner (19521 1962) in his "Wagner Tree" method. Both methods require the evaluation of character states in the particular under study in order to determine trends in evolution. Henning (1950) termed the generalized state as "pleisomorphic" and the derived state "apomorphic" and this terminology will be maintained here. Both methods are designed to examine apomorphic similarities based on the principle that if two taxa have such a character state, their immediate, common ancester will also have it. Both methods allow construction of a phylogenetic diagram (cladogram).

In this present study the Wagner system is used in the study of *Dicranum* and *Orthodicranum* since it provides a method of assigning numerical values to apomorphic character states. The method has previously been used for numerous studies of which those on the Capparidaceae (Iltis, 1959), *Diellia* (Wagner, 1952), *Orthotrichum* (Vitt, 1971), and *Selgeria* (Vitt, 1976) are examples. Methods for computing diagrams have been discussed by Farris (1970). Pleisomorphic character states are assigned a numerical value of zero and apomorphic character states are considered as 1.0. The method also allows for intermediate and highly apomorphic states in which case values of 0.5 and 2.0 are respectively assigned. A total, representing the degree of specialization for the taxon, is then derived, with higher sums indicating the more specialized taxa. Using a series of concentric circles as specialization levels, the taxa relationships can be displayed as dots with more specialized taxa on the outer circles. The dots are connected by the "sister method" at a specialization level indicated by the number of apomorphic states common both taxa. In proceeding through this proccess, it is essential to introduce hypothetical ancestors at specified points. As the character states common to two evolutionary lines indicate their level of connection, hypothetical ancestors can be introduced as long as common apomorphic states exist, thus allowing relationships of widely separated taxa to be visualized.

Before deriving a "Wagner Tree" for *Dicranum* and *Orthodicranum* it was necessary to decide what constitutes a pleisomorphic and apomorphic character state. Although Miller (1971), Vitt (1971), Koponen (1968b), Smith (1975), and Delgadillo (1975) have made several suggestions regarding trends in other groups, I felt the character states in *Dicranum* and *Orthodicranum* should be independently evaluated. Therefore, I have made a number of *apriori* decisions concerning apomorphic states. These decisions were made after all taxa were thoroughly examined in both the laboratory and the field. The major factors influencing the decisions were two: 1) frequency - a character state occurring frequently is species is considered more pleisomorphic than a rarely occuring character state, and 2) association with other character states - a character state commonly occurring with other suspected pleisomorphic states is also taken as pleisomorphic. The majority of these character states are discussed below.

Habitat: Humus and soil (0) are taken as pleisomorphic while wood (logs or living trees) (1.0) represents the apomorphic state. Of the twenty-seven taxa studied, seven grow primarily on wood while thirteen occur primarily on soil or humus. One species, *O. fulvum*, grows primarily on rock (2.0) and is considered an advanced apomorph while six others found on peat (0.5) or extremely sandy soil (0.5) are considered intermediate.

Plant Size: Medium sized plants (0) are considered pleisomorphic while both extremely small (1.0) and extremely large states (1.0) are considered apomorphic. *Dicranum majus* and *D. polysetum* are large while *Orthodicranum montanum* is small. Several species normally slightly larger than *O. montanum* (*O. flagellare*, *O. strictum*, *D. elongatum*) are assigned intermediate values (0.5).

Leaf Shape and Orientation: Leaves of most species studied are lanceolate and straight (0) to slightly falcate-secund (0.5), these conditions are considered pleisomorphic and intermediate while broadly lanceolate (1.0) or ovate-lanceolate (1.0) are taken as apomorphic in shape while those with twisted leaf apices (1.0) are considered apomorphic in orientation. Examples with pleisomorphic leaf shapes are *D. elongatum*, *D. groenlandicum*, *D. undulatum*, and *O. strictum* while the apomorphic state is represented by the twisted leaves of *D. fuscescens*, *D. ontariense*, and *D. condensatum*. The apomorphic state of broadly lanceolate or ovate-lanceolate leaf shape is seen in *D. spadiceum* and *D. amannii*.

Undulations and Papillae: Smooth leaves (0) are considered pleisomorphic while undulate leaves (1.0) are taken as apomorphic. All members of section *Spuria* have undulations on the leaves, as does *D. polsetum*, and some forms of *D. scoparium* (both of section *Dicranum*) and it seems as if this character state has independently evolved in both sections. In addition to undulations, the lamina may be ornamented with papillae. These thickenings are normally over cell lumens however in at least one species, *Dicranum brevifolium*, they are formed by a protrusion of the cell wall between the laminal cells. Smooth laminal and costal cells (0) are considered pleisomorphic, papillae on costal cells (1.0) are taken as apomorphic and such species as *D. sulcatum*, *D. spurium*, and *D. montanum* which have papillae on laminal cells (2.0) are considered highly apomorphic.

Leaf Apex: Most species investigated have leaves with an acute apex with a percurrent or slightly excurrent costa (0) and this condition is thought to be pleisomorphic. Variations from this include narrowly acute apices with a percurrent to strongly excurrent costa (1.0) as seen in *D. sulcatum*, *D. ontariense*, and *D. fuscescens*, or an obtuse apex with a subpercurrent costa (1.0) as seen in *D. undulatum* and *D. groenlandicum*. Both of these states are taken as apomorphic while those species with fragile leaf apicies (*D. fragilifolium*, *O. viride*, *O. strictum*) or cucullate (*D. amannii*) are considered highly apomorphic (2.0).

Laminal Cells and Cell Walls: Long laminal cells (0) are considered pleisomorphic, and short cells are taken as apomorphic. Long cells are found throughout the length of leaves of *D. groenlandicum* and all species of section *Dicranum*. Short cells are found in the remainder of the genus *Dicranum* and in *Orthodicranum* . It seems plausiable that the first species in *Dicranum*'s ancestory had all long cells in the lamina (ie. section *Dicranum*) and gradual divergence produced species with short upper cells (*D. fuscescens*), and still further divergence produced short basal cells (*D. brevifolium*, *O. fulvum*). The cell walls of most Dicrana are thinner than the thickness of the cell lumens (0) and this state is considered pleisomorphic. The apomorphic state exists when the thickness of the wall is essentially equal to that of the lumen (1.0) and is found in *D. elongatum* and *D. groenlandicum*.

Alar Cells: Bistratose alar cell regions (0) are considered pleisomorphic while unistratose regions (1.0) are taken as apomorphic by the proccess of reduction. The latter state is seen in all members of *Orthodicranum* while the former is characteristic of the genus *Dicranum*. In addition, alar cells normally form in the leaf corners and do not extend to the costa (0) as seen in *D. fuscescens* and others. When the alar cells do extend to the costa as in *D. fragilifolium*, they are considered to be in an apomorphic state.

Lamina and Margin Thickness: Both the lamina and laminal margins are normally unistratose (0) in the pleisomorphic state while bistratose conditions (1.0) are considered apomorphic. Bistratose lamina are found in *D. brevifolium* var. *bistratosum* and *O. viride* while occasional bistratose areas are encountered in *D. brevifolium* var. *brevifolium*, *D. majus*, and *O. fulvum*. Bistratose laminal margins (1.0) are found in *D. fuscescens*, *D. sulcatum*, *D. acutifolium*, and *D. brevifolium* while *D. brevifolium* var. *bistratosum* may have a highly apomorphic state of tristratose margins (2.0).

Lamellae: The presence of wing-like projections (1.0) from the abaxial costal surface is considered apomorphic. It is found in members of section *Dicranum* and is absent from the remaining sections. There is a trend within section *Dicranum* indicating character reversal in this state as *D. leioneuron* and *D. amannii* have only remnants of lamellae (2.0). This state is taken as highly apomorphic.

Costa differentation: The number of guide cell rows, the number of stereid cell rows, the size of the stereid lumens, and development of adaxial layer of external cells are all characters of the costa. Pleisomorphic states are one row of guide cells (0); 4 to 6 stereid rows (0); small stereid lumens (0); and undifferentiated cells in the adaxial layer (0). Apomorphic states are respectively two rows of guide cells (1.0) as in *D. majus*; more than 6 rows of stereid cells (1.0) as in *D. sulcatum*; moderately enlarged stereid lumens (1.0) as in *D. brevifolium*; and cells of the abaxial costal layer differentiated from the stereids by having large lumens (1.0) as in *D. muehlenbeckii*. Two species, *D. pallidisetum* and *O. strictum* lack distinguishable stereid cells (2.0) and are considered highly apomorphic.

Sexual Condition: All species of *Dicranum* and *Orthodicranum* are dioicous yet a number of species have reduced male gametophytes and may be referred to as pseudomonoicous. Loveland (1956) considered this state the result of hormonal influences from the female gametophyte because spores germinating on female tomentum and leaves would produce reduced males while spores from the same capsule would produce full sized males if allowed to germinate independent of the female. I consider those species capable of producing reduced or "dwarfed" males as apomorphic (1.0).

Setae Number: Polysetae has been most recently studied by Koponen (1968b) in the genus *Plagiomnium* and was prevously discussed by such authors as Sowter (1948), Dalby (1959), Chopra and Sharma (1958), and Longston (1962). Chopra and Sharma (l.c.) associated polysetae with polyploidy in the genus *Atrichum*; however, Koponen (1968b) found no correlation of this type in *Plagiomnium* as only two of seven taxa studied were polyploid. Koponen concluded polysetae is the result of "some kind of regulative mechanism" that has been disrupted. He did not discuss which state he considered to be more advanced. As a permanent disruption (genetic change) would explain polysetous species, and monosetae is the common state, I am considering polysetae (1.0) to be apomorphic. In *Dicranum* it is found in *D. majus*, *D. ontariense*, and *D. polysetum*.

Capsule Size and Shape: Large capsules (0) are taken as pleisomorphic while small capsules (1.0) are considered apomorphic. The latter state is found in such species as *D. elongatum*, *D. groenlandicum*, and *D. angustum*. Capsule shape, curved (0) in the pleisomorphic state and straight (1.0) in the apomorphic state, is one of the important characters used to distinguish *Orthodicranum* as all five species have erect capsules. All species of *Dicranum* except *D. groenlandicum* and *D. rhabdocarpum* have curved capsules.

Capsule Neck: The common and pleisomorphic state in *Dicranum* and *Orthodicranum* is a short neck which constricts to the setae attachment just below the spore sac. Apomorphic conditions (1.0) exist when the neck is somewhat larger as found in section *Muehlenbeckia* or when a struma is present. The struma is most highly developed in such species as *D. fuscescens* and *D. sulcatum*, members of section *Fuscescentiformia*; and *D. condensatum* and *D. spurium* of section *Spuria*.

Capsule Ribbing: When dry, all capsules of *Dicranum* and *Orthodicranum* contract somewhat producing various striations on the walls. Species of *Dicranum* produce rather uniform ribs while *Orthodicranum* species produce loosely arranged wrinkles. It seems plausable that uniform ribbing is pleisomorphic (0) whereas the smoother capsules are apomorphic (1.0). Since *Orthodicranum* species grow primarily on wood and maybe found on vertical surfaces, it can be seen that strong ribbing is no longer necessary to force spores to the mouth of the capsule.

Annulus: The highly specialized nature of the annulus suggests that it has evolved only once in ancestral bryophytes. As most *Dicranum* and *Orthodicranum* species have an annulus, it must have been present in their ancestors and later lost by the process of reduction. *Orthodicranum strictum* and all members of *Dicranum* section *Dicranum* (except *D. angustum*) are without an annulus. I considered this state to be apomorphic (1.0) and the presence of an annulus to be pleisomorphic (0).

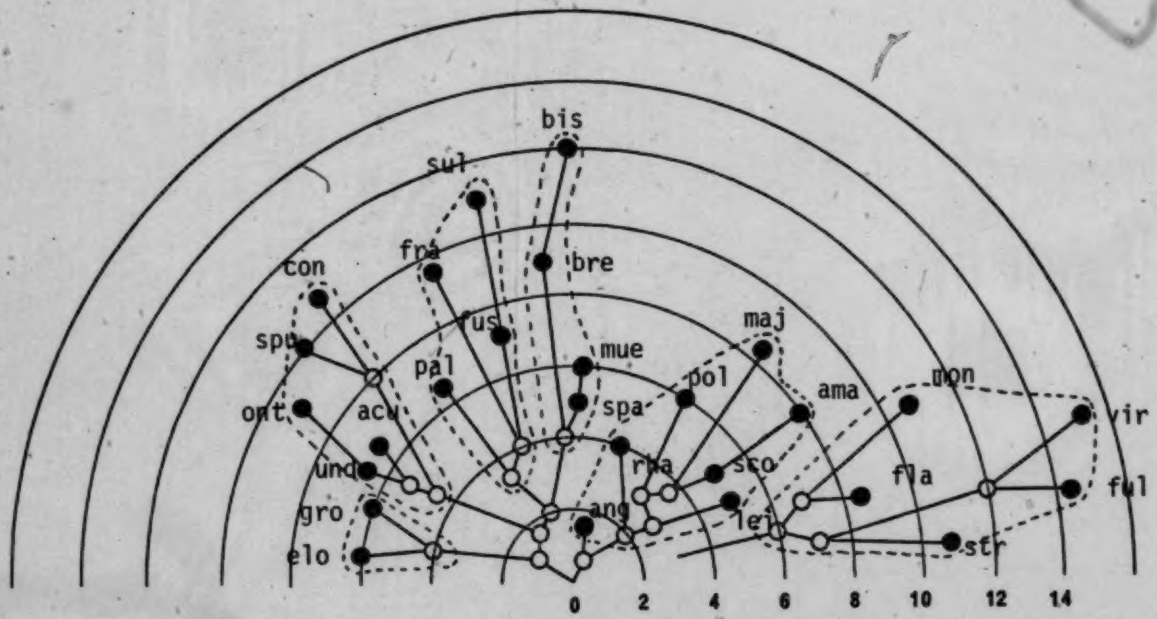
Asexual Reproduction: Three species regularly reproduce asexually by fragile leaf apecies; however, that character state is considered under development of the apex shape and would cause abnormal bias if considered again. Three additional species may be considered apomorphic in this respect since the produce either attenuated stem tips (0.5) as seen in *D. leioneuron* and *D. scoparium*, or specialized branches that fragment (1.0) as seen in *O. flagellare*.

Endemism: All six taxa endemic to North America seem to have been autochthonously derived from widespread relatives instead of being relicts equal in age to the other taxa. As a consequence, I have considered endemic taxa to be apomorphic (1.0) and the widespread taxa to be pleisomorphic (0) in this respect.

The resultant "Wagner" diagram indicating the proposed relationships of *Dicranum* and *Orthodicranum* species is shown in Fig. 83. By examining the diagram several evolutionary trends can be seen and a hypothetical picture of the ancestorial type can be made. The basic ancestor to the *Dicranum-Orthodicranum* complex was probably quite similar to *Dicranum angustum* in that the laminal cells were long with little or no pitting, an annulus was present on a ribbed, curved capsule, and the abaxial costal surface was without lamellae. In contrast to *D. angustum*, it had serrate laminal margins, a lightly ribbed or wrinkled capsule, and male plants equal in size to the female plants. It probably grew on humus in a mesophytic forest habitat.

Of the various segregations occurring in the complex, one of the first was probably of laminal cell length; a decrease in cell length would lead to all *Dicranum* species in sections *Spuria*, *Fuscescentiformia*, and *Muehlenbeckia*, and an increase would lead to species in section *Dicranum*. From this basic division, several major lineages have developed, each emphasizing different characters. As the degree of emphasis varies within each section of *Dicranum* as well as in *Orthodicranum*, I will discuss the trends of each group independently.

FIGURE 83. A Wagner Diagram of the species of *Dicranum* and *Orthodicranum* found in North America. Solid circles (●) represent extant species and open circles (○) represent hypothetical ancestors. The dotted lines circumscribe the genus *Orthodicranum* and the sections of *Dicranum*. The three letters are the first of the specific epithet except for *D. brevifolium* var. *bistratosum* where the first letters of the variety name are used.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Section *Dicranum* Hedw.: This is the most primative group in the genus *Dicranum*. All species grow on humus or soil and all species have long laminal cells. Since separation from the other sections which now have short upper cells, two major changes have occurred in this group: 1) lamellae were developed on the abaxial costal surface, and 2) the annulus was lost by reduction. The lamellae development is at its highest point in specimens of *D. scoparium* and *D. polysetum* and seems to be in a reduction trend in such species as *D. leioneuron* and *D. amannii*. Other evolutionary trends distinguishable in this section are: 1) monosetae toward polysetae, 2) increased wall pitting, 3) a single row of guide cells toward a double row, and 4) a reduction in male gametophyte size.

Section *Fuscescentiformia* Kindb.: All members of this group have short upper laminal cells and produce an annulus; therefore, the ancestor of this group must have separated from the long-celled stock before the annulus was lost. Three of the four species in this group have adapted to wood habitats while the fourth has adapted to soil of the subalpine. Other trends in the section include: 1) development of papillose laminal cells, 2) a tendency toward excurrent costae, 3) increase in leaf twisting and 4) increase in the number of stereid rows. Although the trend in the group seems to be toward a stronger costa, *D.*

pallidisetum does not have bands of stereid cells. As this state is found in only one species of *Dicranum* (and one of *Orthodicranum*) it must be considered apomorphic. However, since *D. pallidisetum* has few apomorphic characters in common with the remaining species of section *Fuscescentiformia*, it can be concluded that this species diverged from the main line somewhat earlier than the others.

Section *Spuria* B.S.G.: This is also a group of species with short upper cells and a capsule that produces an annulus. All species grow on soil, humus or peat and the following trends are indicated: 1) a tendency for polysetae, 2) a reduction of male gametophyte size, 3) a development of papillose cells, 4) a tendency for falcate-secund or twisted leaves, 5) a development of undulate leaves, 6) a shortening of basal cells, and 7) a tendency for irregular areolation patterns in the lamina. The original member of this section would have been similar to the extant *D. undulatum*.

Section *Muehlenbeckia* Peterson: The members of this section, like those in section *Fuscescentiformia*, show evolutionary divergence in internal costal anatomy. The stereids are different than those found in any other complex and there is a tendency toward development of large lumens in the cells of the adaxial costal layer. Other trends include: 1) development of a long neck on the capsule,

2) development of bistratose laminae, 3) decrease in basal cell length, and 4) a tendency toward more ovate-lanceolate leaves.

Section *Elongata* Hag.: This section contains only two species. *D. elongatum* and *D. groenlandicum*, with the former having short upper cells and the latter having long ones. Although it may seem inconsistant putting the two in the same section when upper cell length is a major criterion for separating other sections, there other similarities that indicate the two species do belong together as a unit, and separate from the other sections. Both species show the following trends: 1) development of thick laminal cell walls (usually the distance between cell lumens is about equal to the width of the lumen), 2) reduced capsule size, and 3) a thick, matted growth habit. In addition, both species produce an annulus indicating that they have evolved from ancestors with short upper cells and negating the possibility that *D. groenlandicum* is derived from the long-celled, exannulate line of section *Dicranum*.

Orthodicranum: This genus is composed of five species in North America, four of which possess an annulus. This highly elaborate structure probably evolved only once at a time prior to this groups separation from *Dicranum*. It seems plausible that both *Orthodicranum strictum* and *Dicranum* section *Dicranum* lost the annulus independently from one another. Also, the group produces erect, smooth capsules, unistratose alar cells, and has a tendency for production of specialized branches for asexual reproduction. None of these apomorphic states are found in any member of *Dicranum* with short upper cells. As a result, *Orthodicranum* precursors must have separated from the *Dicranum* complex at a point in time prior to divergence of the sectional ancestors in *Dicranum*. The evolutionary trends seen in the genus include: 1) a specificity for habitats of wood (occasionally rock), 2) a tendency for asexual reproduction, usually by fragile leaf tips, 3) development of erect capsules, 4) a reduction in alar cell layers, and 5) a decrease in peristome teeth width. In addition to these trends that are found in all five species, there are other trends that indicate three major lines of evolution within *Orthodicranum*. *Orthodicranum strictum* has lost the annulus and stereid cells indicating a major divergence from the other four. *O. fulvum* and *O. viride* have evolved a broader costa and short basal cells while the remaining two (*O. flagellare* and *O. montanum*) have maintained a narrow costa and relatively long basal cells.

Evolution of Character States in Association with Habitat: Since a variety of habitats are occupied by *Dicranum* and *Orthodicranum* species, it is essential to discuss character states that correlate with particular habitats. Such substrate types as rock, peat, and sand have been adapted to by *Dicranum* species; however, the number of species occurring in each habitat is too small to enable a correlation with character states. Other such substrates as humus, wood, and tundra are occupied by more species. Species found to commonly grow on humus or soil at lower elevations are usually large species (*D. majus*, *D. polysetum*, *D. scoparium*, and *D. ontariense*) that are loosely matted together with dense tomentum. They show a tendency toward polysetae and regularly produce dwarfed males. Those species occurring on humus or soil at higher elevations (*D. muehlenbeckii*, *D. pallidisetum*, and *D. rhabdocarpum*), are smaller, have shorter more broadly-lanceolate leaves, and tend to grow in compact tufts. Similarly, species found to commonly occur in tundra habitats (*D. elongatum*, *D. groenlandicum*, *D. angustum*, *D. acutifolium*, *D. ammannii*, and *D. spadiceum*) show tendencies toward: 1) reduced gametophyte size, 2) reduced capsule size, 3) compact growth habits, 4) acute to broadly acute leaf apices, 5) broadly lanceolate or ovate-lanceolate leaves, and 6) smooth laminal surfaces. Species common to wood substrates generally have: 1) an excurrent costa or long narrowly lanceolate leaves (*D. fuscescens*, *D. sulcatum*, *D. fragilifolium*, *O. strictum*, *O. viride*), 2) abundant papillae on the costa and usually on the lamina, and 3) serrate margins (*D. fuscescens*, *D. sulcatum*, *O. montanum*, *O. viride*, and *O. flagellare*) Also, the erect, smooth capsules of all *Orthodicranum* species are probably a result of growth on vertical surfaces. In such places the capsule would be positioned horizontally and neither curvature nor strong constriction would be necessary to disperse spores.

Taxometric Map: A number of methods have been developed to examine similarities expressed by various organisms, including those discussed by Kruskal (1964), Sneath (1966), Sokal and Sneath (1964), Wirth *et al.* (1966), and Carmichael *et al.* (1968). I have selected a method that produces a "cluster analysis" by examining similarities that exist between OTU's (species in this case) based on presence or absence of character states. The computerized program "Taxmap" (Carmichael and Sneath, 1969; Carmichael, 1978) compares the OTU's, groups them into similar clusters, and draws a diagram depicting their multidimensional relationships. Character states may be weighted to emphasize certain states that are sequential (i.e. leaf shapes of lanceolate, broadly-lanceolate, and ovate-lanceolate can be a series). In applying this system to *Dicranum* and *Orthodicranum*, the data in Table 12 was used in order to facilitate comparison of the phenetic approach of "Taxmap" and the phylogenetic method of the "Wagner Tree".

	Character	*D. angustum*	*D. rhabdocarpum*	*D. leiomeuron*	*D. scoparium*	*D. spadiceum*	*D. muehlenbeckii*	*D. polysetum*	*D. groenlandicum*	*D. elongatum*	*D. pallidisetum*	*D. acutifolium*	*D. undulatum*	*D. fuscescens*	*D. howellii*	*D. majus*	*O. flagellare*	*D. brevifolium*	*D. ontariense*	*D. fragilifolium*	*D. spurium*	*D. condensatum*	*D. sulcatum*	*O. strictum*	*O. montanum*	*D. brevifolium* var. *bistratosum*	*O. fulvum*	*O. viride*	Pleisomorphic/Apomorphic States
1.	Habitat	-	-	.5	-	-	-	-	.5	.5	-	-	.5	1	-	-	1	-	-	1	.5	.5	1	1	1	-	1	2	Humus (0), Peat or Sand (.5), Wood (1), Rock (2)
2.	Plant Size	-	-	-	-	-	-	1	.5	.5	-	-	-	-	-	1	.5	-	-	-	-	-	-	.5	1	-	.5	.5	Medium (0), Small or Large (1)
3.	Leaf orientation	-	-	-	.5	.5	.5	-	.5	.5	.5	.5	-	1	-	.5	1	.5	.5	-	-	1	1	-	1	.5	1	-	Straight (0), Falcate-secund (.5), twisted (1)
4.	Leaf shape	-	-	.5	-	.5	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	Lanceolate (0), ovate or broadly lanceolate (1)
5.	Leaf attachment	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	.5	-	-	-	1	-	-	Erect (0), arching from stem (1)
6.	Undulations	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	Absent (0), present (1)
7.	Apex shape	-	-	-	-	-	-	-	1	-	-	-	1	-	2	-	-	-	1	2	-	-	1	2	-	-	1	2	Acute (0), obtuse or excurrent (1), fragile or cucullate (2)
8.	Margins	1	-	.5	-	-	-	-	.5	.5	-	.5	-	-	1	-	-	-	-	.5	-	-	-	.5	-	-	-	-	Toothed (0), entire (1)
9.	Upper cells	-	-	-	-	1	1	-	-	1	1	1	1	1	-	-	1	1	1	1	1	1	1	1	1	1	1	1	Long (0), short (1)
10.	Basal cells	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	.5	-	-	-	1	1	1	Long (0), short (1)
11.	Wall thickness	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Thin (0), thick (1)
12.	Alar cells	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.5	-	1	-	-	-	-	-	.5	.5	.5	Not reaching costa (0), extending to costa (1)
13.	Wall pitting	-	-	-	-	.5	.5	-	-	1	1	.5	.5	1	-	-	1	1	.5	1	.5	.5	1	1	1	1	1	1	Pitted (0), not pitted (1)
14.	Costa width	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	Narrow (0), wide (1), extremely wide (2)
15.	Alar layers	-	.5	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	-	1	1	Bistratose (0), unistratose (1)
16.	Margin layers	-	-	-	-	-	-	-	-	-	-	.5	-	1	-	1	-	1	.5	-	-	.5	1	-	-	2	1	1	Unistratose (0), bistratose (1)
17.	Lamina layers	-	-	-	-	-	-	1	-	-	-	-	-	-	-	.5	-	-	-	-	-	-	-	-	-	1	.5	.5	Unistratose (0), bistratose (1)
18.	Papillae	-	-	-	1	-	-	-	-	-	1	1	1	1	-	1	-	1	1	-	2	2	2	-	2	1	1	1	Absent (0), on costa (1), on costa and lamina (2)
19.	Lamellae	-	1	2	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	Absent (0), present (1), reduced(2)
20.	Guide cells	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	One row (0), two rows (1)
21.	Stereids	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	4 to 6 rows (0), more (1)
22.	Stereid lumens	-	-	-	-	1	1	-	-	-	2	-	-	-	-	-	-	1	-	2	-	-	-	-	-	1	-	-	Small (0), large (1), cells absent (2)
23.	External row	-	-	-	-	.5	1	-	-	-	-	-	-	-	-	.5	-	-	-	-	-	-	-	-	-	-	-	-	Not differentiated (0), differentiated (1)
24.	Sexual state	.5	-	-	1	-	-	1	-	-	-	1	1	-	1	1	-	-	1	-	1	1	-	-	-	-	-	-	Dioicous (0), pseudomonoicous (1)
25.	Setae	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	Monosetous (0), polysetous (1)
26.	Capsule size	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	Large (0), small (1)
27.	Capsule shape	-	.5	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	-	1	1	Curved (0), straight (1)
28.	Struma	-	-	-	-	-	-	-	-	-	-	.5	.5	1	-	-	-	-	.5	1	1	1	1	-	-	-	-	-	Absent (0), present (1)
29.	Neck	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	Short (0), long (1)
30.	Ribbing	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	-	1	1	Ribbed (0), wrinkled (1)
31.	Annulus	-	1	1	1	-	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1	-	-	-	-	Present (0), absent (1)
32.	Asexual rep.	-	-	.5	.5	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	Absent (0), present (1)
33.	Endemism	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	1	-	-	1	-	-	Not endemic (0), endemic (1)
	TOTAL	1.5	4.0	5.0	5.0	5.0	6.0	6.0	6.0	6.0	6.5	6.5	6.5	7.0	8.0	8.5	8.5	9.0	9.0	9.5	10.0	10.5	11.0	11.0	11.0	12.0	14.5	15.5	

Table 12. The twenty-seven taxa of *Dicranum* and *Orthodicranum* in North America and thirty-three characters used in the phylogenetic and phenetic analyses. The numbers indicate apomorphic character states and the totals represent relative advancement of the taxa.

Figures 84 and 85 are graphical displays of this system applied to the data in Table 12. Figure 84 is an equally weighted comparison while Fig. 85 represents weighted characters. The circles on the figures are clusters of OTU's with the diameter of the circle representing a scalar distance between the two most distant OTU's within. The lines connecting clusters represent scalar distances between clusters, the isolated points are individual OTU's. Arrows point toward a cluster's closest neighbour.

Figure 84, the unweighted analysis has divided *Dicranum* and *Orthodicranum* into four clusters and two isolated OTU's. Cluster number 1 contains all members of *Orthodicranum*, cluster number 4 contains six of the seven species in *Dicranum* section *Dicranum* and isolated OTU number 6 (*D. majus*) is shown as as closest to cluster number 4. Cluster number 3, the largest of the group, contains most members of *Dicranum* with short upper cells, that is, sections *Fuscescentiformia*, *Spuria*, *Elongata*, and *Muehlenbeckia*. Cluster number 2 (*D. brevifolum* varieties) and isolated OTU member 5 (*D. fragilifolium*) are indicated as being close to cluster number 3.

Figure 85, the weighted analysis has separated the same data into nine clusters, three of which are isolated OTU's. Cluster number 1 contains all members of *Orthodicranum*, cluster number 4 is all members of *Dicranum* section *Dicranum* except for *D. majus* (isolated OTU number 8) which is again shown closest to cluster number 4. Clusters 2, 3, 5, 6, 7, and 9 contain the taxa of *Dicranum* with short upper cells. Cluster 2 represents both

FIGURE 84. Taxometric map of the North American *Dicranum* and *Orthodicranum* species based on unweighted data. The diameter of the circles represents the maximum distance between any pair of species included in the cluster. The lines connecting the margins of the circles represent the distance between the nearest neighbors in the two clusters. Each cluster is shown the proper distance from its two nearest neighbors. To fit the cluster into two dimensions, other distances may be distorted. The arrows indicate the nearest neighbor to each cluster. The letters represent the first three letters of the specific epithet for all *Orthodicranum* and *Dicranum* species except for "bis" which are the first three letters of the variety name. Scale: 1 cm = 49 units.

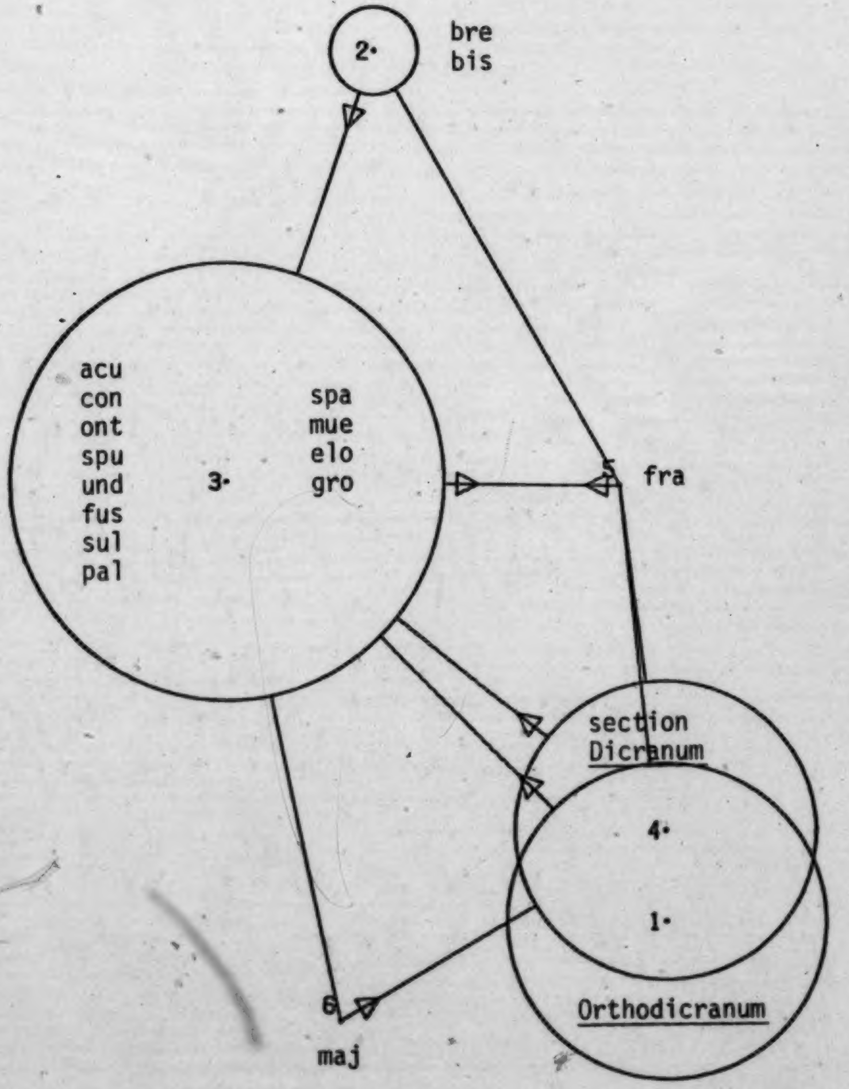
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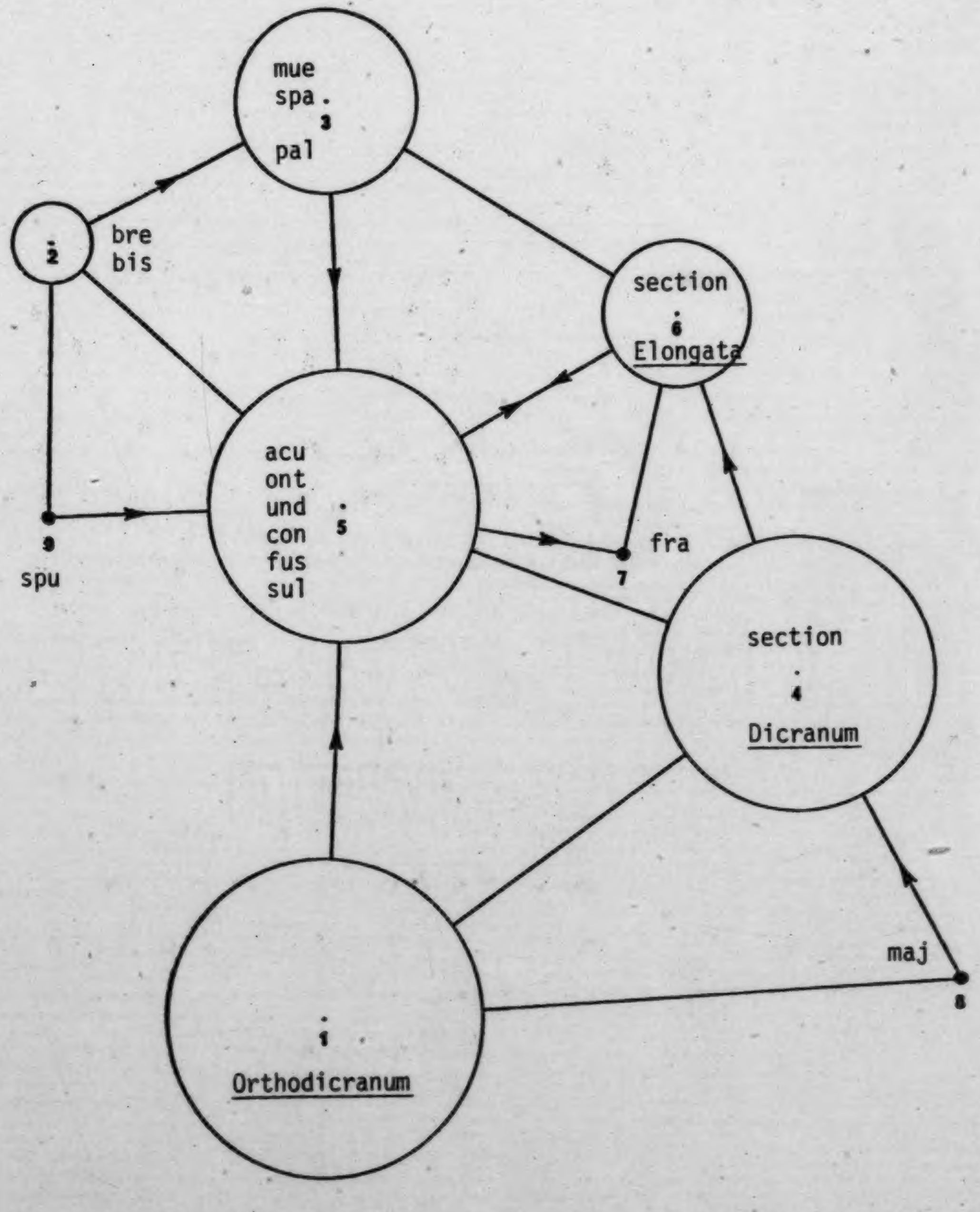
FIGURE 85. Taxometric map of the North American *Dicranum* and *Orthodicranum* species based on log weighted data. The diameter of the circles represents the maximum distance between any pair of species included in the cluster. The lines connecting the margins of the circles represent the distance between the nearest neighbors in the two clusters. Each cluster is shown the proper distance from its two nearest neighbors. To fit the cluster into two dimensions, other distances may be distorted. The arrows indicate the nearest neightbor to each cluster. The letters represent the first three letters of the specific epithet for all *Orthodicranum* and *Dicranum* species except for "bis" which are the first three letters of the variety name. Scale: 1 cm = 49 units.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varieties of *D. brevifolium* which, by the arrow, is shown closest to cluster number 3 (*D. muehlenbeckii*, *D. spadiceum*, and *D. pallidisetum*). These two clusters, excluding *D. pallidisetum*, compose section *Muehlenbeckia*. Cluster number 5 contains four of five members of section *Spuria* as well as *D. fuscescens* and *D. sulcatum* while the fifth number of section *Spuria* (*D. spurium*) is represented by isloated OTU number 9 and shown closest to cluster 5. Cluster 6 contains section *Elongata* members *D. elongatum* and *D. groenlandicum* while isolated OTU number 7 (*D. fragilifolium*) is shown as intermediate between clusters 5 and 6.

Both weighted and unweighted comparison methods indicate the genus *Orthodicranum* and *Dicranum* section *Dicranum* to be distinct units. *Dicranum majus* is placed separate, but in both cases it is closest to section *Dicranum*. The two comparisons differ primarily on the segregation of the species of *Dicranum* with short upper cells in that the unweighted analysis placed the majority of the species in a single cluster while the weighted analysis divided them into smaller units. Since the unweighted method only examines similarities in character states, it is understandable why all of these species which have short upper cells, curved capsules, and an annulus would be clustered together. The isolated OTU number 5 (*D. fragilifolium*) and cluster number 2 (*D. brevifolium* varieties) are separated from the main cluster of species with short upper cells since the former lacks stereids and has broken leaf apices, and the latter contains two closely related varieties, one of which has bistratose areas in the lamina. The smaller clusters indicated by the weighted analysis are similar to the taxonomic sections recognized in this treatment. *Dicranum elongatum* and *D. groenlandicum* are seen as a distinct unit and the closely related clusters 2 and 3 represent section *Muehlenbeckia*. *Dicranum pallidisetum* is included in cluster 3 because of gametophytic similarities to *D. muehlenbeckii*, even though sporophytically it is similar to *D. fuscescens*. Section *Spuria*, except for *D. spurium*, is contianed in cluster 5 along with *D. fuscescens* and *D. sulcatum*. *Dicranum spurium* is placed closest to cluster 5 indicating affinities with it. Section *Fuscescentiformia*, as recognized in this treatment, is severed into several units as *D. pallidisetum* is placed within cluster 3, *D. fuscescens* and *D. sulcutum* are in cluster 5, and *D. fragilifolium* is an isolated OTU.

Both the Wagner Tree Method and the Taxometric Method of examining the interspecific relationships indicate the section *Dicranum* to be a distinct group with *D. majus* being the least similar of the seven species. Both methods recognize the section *Elongata* and to some extent the sections *Spuria* and *Muehlenbeckia*. The Wagner Tree Method, which considers evolutionary trends, separates out section *Fuscesaentiformia*, while the Taxometric method, which examines phenetic similarities, does not recognize it. Nevertheless, I believe section *Fuscescentiformia* to be distinct since the species are all very similar in sporophytic character states, habitats and laminal cell patterns.

The most significant point resulting from this comparison is that the Wagner Tree and both Taxometric maps indicate *Orthodicranum* to be distinct. The former method allows for comparison of apomorphic character states and has resulted in a hypothetical link of all *Dicranum* species at the zero level of specialization. There are no apomorphic states common to *Dicranum* and *Orthodicranum* to indicate a similar connection. Both taxometric maps link *Orthodicranum* to the *Dicranum* species with short upper laminal cells; however, the connection as seen in the weighted map is more tenuous than any other connection. I consider this to be supportive to the segregation of *Orthodicranum* since the method of analysis does not emphasize all pleisomorphic-apomorphic trends and yet it still separates the group to a further degree than shown for any other cluster.

CONCLUSIONS

Dicranum and *Orthodicranum* are two genera of the Dicranaceae, a family of acrocarpous mosses characterized as having a haplolepidous peristome composed of teeth normally divided a portion of their length into two segments. These two genera are predominant in the boreal-arctic habitats where they have specialized into microhabitats of logs, humus, soil, and peat. The genera *Campylopus* and *Dicranoloma* occupy similar niches in the southern hemisphere. Other close relatives include the autoicous genera *Arctoa, Kiaeria, Oncophorus,* and *Cynodontium*; and *Chorisodontium* with its precociously germinating spores. All of these were included within Hedwig's original concept of the genus *Dicranum*.

This investigation has shown that the genera *Dicranum* and *Orthodicranum* are old groups that evolved long ago. Most of the extant species were probably in existance during the early Tertiary and many were members of a once widespread, possibly circumboreal, flora. Only five species and one variety of the North American Dicrana have evolved in more recent times and all six taxa are endemic to small portions of the continent.

The ancestor to this complex may be visualized as having long laminal cells, an acute leaf apex with a percurrent costa, no lamellae or papillae, serrate laminal margins, a curved, ribbed capsule that produced an annulus, and male plants equal in size to the female plants. It grew on soil or humus in mesic forests. Of the extant species, *D. angustum* is most similar to this form. During the time before the breakup of Laurasia (65 million years ago) there was considerable adaptive radiation in the *Dicranum* group with at least three major evolutionary lines diverging from one another. One, which maintained long upper laminal cells, remained on a humus habitat and evolved at a relatively slow rate, becoming the present section *Dicranum*. One of the first evolutionary modifications was the loss of the annulus, and today, all members of the section except *D. angustum* are without this structure. Secondly, there was a development of lamellae on the surface of the costa. It is possible the added surface area increased the photosynthetic ability of the plant. Parallel structures occur in other such genera as *Polytrichum*, *Oligotrichum*, *Aloina* and *Crossidium*. The lamellae would not be a detriment to water retention as the humid nature of the forest habitat would maintain a high humidity level. A reversal of this trend is seen in species that have evolved into more northern habitats. *Dicranum amannii* and *D. leioneuron* both have secondarily reduced lamellae which are often no more than slightly enlarged cells of the abaxial costa layer.

The other two groups to diverge from the initial ancestor developed short upper laminal cells and adapted to other habitats. One of these, the ancestor to the extant genus *Orthodicranum* would have colonized logs. As a result, selective pressures have caused this group to diverge along considerably different lines than the other groups. There was a slight reduction in gametophyte size, probably a result of the additional elevation provided by the substrate. Under such conditions, the plants would have been in an advantageous position for spore dispersal and it would no longer be necessary to produce tall plants to extend above other vegetation. In addition, there was a development of asexual reproductive structures, probably because those populations capable of producing these structures could quickly colonize adjacent habitats, thus outcompeting the populations that only reproduced by spores. Many of these colonies would have grown on vertical surfaces and therefore, a curved capsule would not be advantageous to spore dispersal since the spores might actually be cupped within the curve of the capsule. Selective pressure under such circumstances would lead to straight capsules with smooth walls because the strong ribbing would no longer be necessary to force spores to the capsule mouth, as they would fall out by force of gravity.

The other sister group that evolved with short upper laminal cells was probably the first to adapt to drier soils and humus, and the shortened cells probably enhanced this by increasing leaf twist and thereby conserving moisture. The additional cross-wall space found in leaves of this type should provide more areas of differential drying which would result in different rates of tissue contraction and a twisting of the leaf. Four subgroups have evolved from this evolutionary line, with each adapting to different habitat requirements. The first to diverge was the precursor to the section *Elongata* which adapted to open tundra habitats by evolving a compact growth habit and a reduced sporophyte. In such climatic conditions as are found in arctic and alpine habitats, considerable reproduction is the result of gametophytic fragmentation, and spore production is not vital. Similar asexual reproduction occurs in arctic vascular plants. Of the other three subgroups discussed, one partially adapted to a xylicolous habitat (section *Fuscescentiformia*), one remained partially confined to humus in forests (section *Spuria*), and the other evolved into a habitat of exposed soil in the subalpine (section *Muehlenbeckia*).

After the ancestors to section *Elongata* separated the next division probably resulted in the establishment of the precursor to section *Spuria*. This taxon soon separated into two species; *Dicranum undulatum* in mire habitats, and *D. spurium* on moderately sandy soil. As these two species diverged from one another they became circumboreal in distribution and were the only two species in this section until the affects of Pleistocene glaciation created conditions suitable for evolution of at least three additional species. Two of these species, *D. condensatum* and *D. ontariense* are neoendemics of North America while a third species, *D.*

acutifolium survived in Beringia and is now found in Eurasia as well as in North America. A fourth species, *D. drummondii* C. Müll., apparently evolved from the same complex in Eurasia and is a neoendemic of that area.

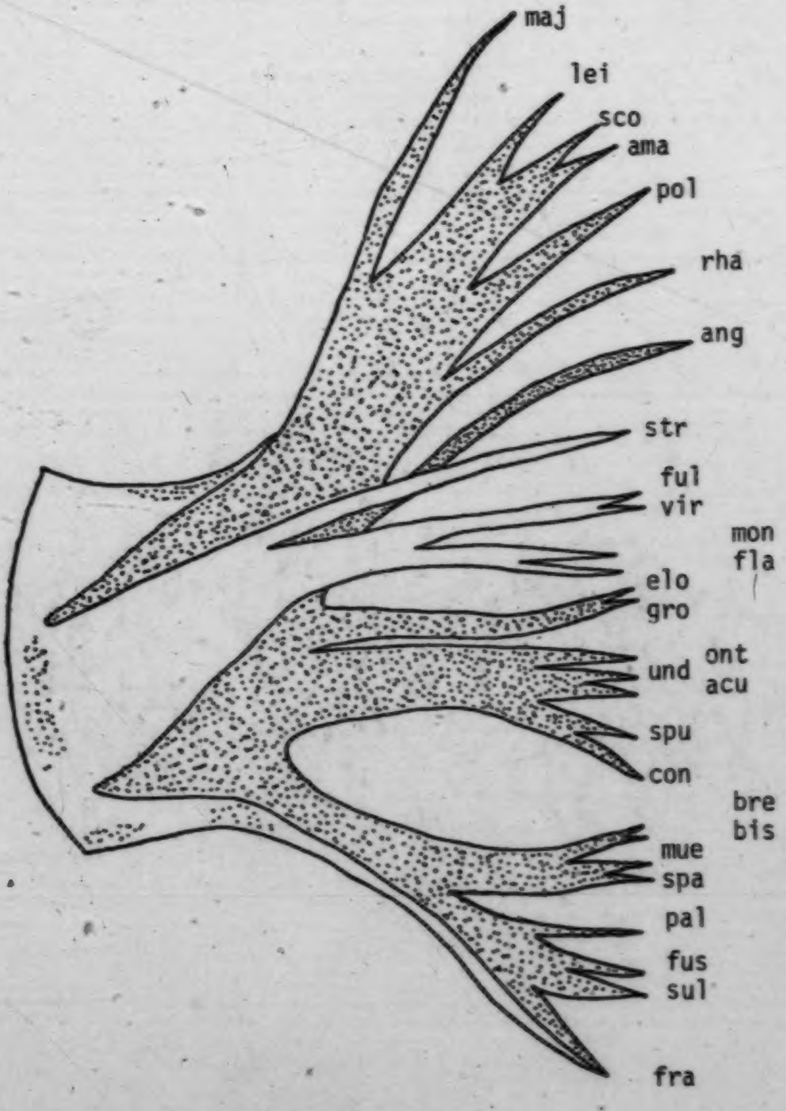
The precursor to section *Muehlenbeckia* evolved into an exposed subalpine habitat. Selective pressures have caused members of this group to develop dense tomentum, broad entire leaves, and stereid cells with large lumens; all characters which probably enable the plants to conserve water. The dense tomentum could act as a sponge; the leaf shape could act as a reservoir; the entire leaf margin could reduce evaporation; and larger lumens could contain more water internally. One variety, *D. brevifolium* var. *bistratosum* is endemic to the Rocky Mountains of Canada and is probably the most recently evolved taxon in the genus *Dicranum*.

The remaining subgroup with short upper laminal cells resulted from adaptation to logs within colder montane forests. The ancestor to section *Fuscescentiformia* adapted to the xylicolous habitat and as a result, some members of the section show trends seen in the genus *Orthodicranum*. These are a reduction in gametophyte size, and asexual reproduction by fragile leaf apices. Since the adaption to wood occurred long after that of the *Orthodicranum* line, selective pressures could not be expected to have had the same degree of effect on the section *Fuscescentiformia*. Future evolution in this group should parallel that of *Orthodicranum*. Asexual reproduction may become more prevalent, the capsules may become more erect, the

the capsule walls should become smooth and the peristome should be eliminated. The last point has not occurred even in the genus *Orthodicranum* but the teeth are somewhat narrower in the group, and other such moss genera as *Orthotrichum, Amphidium,* and *Gymnostomum* (all of which grow on vertical surfaces) either have reduced or missing peristomes.

The forgoing conclusions on the divergence and development of the sections and species of *Dicranum* and *Orthodicranum* have enabled me to produce a hypothetical diagram of the evolution of the group as I envision it. This is presented in Figure 86.

FIGURE 86. A hypothetical evolutionary tree of the species of *Dicranum* and *Orthodicranum* that occur in North America. The letters are the first three letters of the specific epithets of the species of *Orthodicranum* and *Dicranum* except for "bis" which are the first three letters of a variety name.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LITERATURE CITED

Abramova, A.I. and B.I. Dildarin. 1969. *Crumia latifolia* (Kindb.) Schof., in the moss flora of the U.S.S.R. *Biol. Zurn.* 22: 43-48.

Ahti, T. and P. Isoviita. 1962. *Dicranum leioneuron* Kindb. and the other *Dicranum* mosses inhabiting raised bogs in Finland. *Arch. Soc. Zool. Bot. Fenn. 'Vanamo'* 17: 68-79.

Ahti, T., P. Isoviita and W.S.G. Maass. 1965. *Dicranum leioneuron* Kindb. new to the British Isles and Labrador, with a description of the sporophyte. *Bryologist* 68: 197-201.

Allison, K.W. 1952. New records of northern hemisphere mosses in New Zealand. *Trans. R. Soc. New Zeal.* 88: 9-12.

Amann, J. 1912. Flore Des Mousses de la Suisse. II. Lausanne.

Anderson, L.E. 1962. Chromosome numbers: Bryophytes. pp. 45-57 *in* P.L. Altman and D.S. Ditmer (eds.). Growth including reproduction and morphological development. Federation of Amer. Soc. for Exp. Biol., Washington.

Anderson, L.E. 1971. Geographical relationships of the mosses of the Southern Appalachian Mountains *in* P.C. Holt (ed.). The distributional history of the biota of the Southern Appalachians. Part II. Flora. Va. Poly. Inst. & State Univ., Res. Div. Monograph 2: 101-113.

Anderson, L.E. and V.S. Bryan. 1958. Chromosome numbers of some mosses of eastern North America. *J. El. Mitchell Sci. Soc.* 74: 173-199.

Anderson, L.E. and H.A. Crum. (1958) 1959. Cytotaxonomic studies on mosses of the Canadian Rocky Mountains. Bull. Natl. Mus. Canada 160: 1-89.

Anderson, L.E. and R.H. Zander. 1973. The mosses of the southern Blue Ridge Province and their phytogeographic relationship. *J. El. Mitchell Sci. Soc.* 89: 15-60.

Andrews, A.L. 1938. The North American Atlantic species of *Sphagnum*. *Ann. Bryol.* 11: 15-20.

Barnes, C.R. 1890. *In* Röll, J. Vorlaüfige Mittheilungen über die von im Jahre 1888 in Nord-Amerika gasammelten neuen Arten und Varietaten der Laubmoose. *Bot. Centralbl.* 44: 386.

Bartram, E.B. 1933. Manual of Hawaiian Mosses. Bernice P. Bishop Mus. Bull. No. 101: i, 3-275.

Billings, W.D. and L.E. Anderson. 1966. Some microclimatic characteristics of habitats of endemic and disjunct bryophytes in the southern Blue Ridge. *Bryologist* 69: 79-95.

Brassard, G.R. 1967. A contribution to the bryology of Melville Island, N.W.T. *Bryologist* 70: 347-351.

Brassard, G.R. 1970. The relict occurrence of *Seligeria pusilla* in Arctic Canada. *Canad. J. Bot.* 48: 617-619.

Brassard, G.R. 1971. The mosses of northern Ellesmere Island, Arctic Canada. II. Annotated list of the taxa. *Bryologist* 74: 282-311.

Brassard, G.R. and W.C. Steere. 1968. The mosses of Bathurst Island, N.W.T., Canada. *Canad. J. Bot.* 46: 377-383.

Braun, E.L. 1950. Deciduous forests of eastern North America. Philadelphia.

Bridel, S.E. 1819. Muscologiae recentiorum supplementum. IV. Seu Mantissa generum specierumque muscorum frondosorum universa. Methodus nova muscorum ad naturae normam melius instituta et Muscologiae recentiorum accommodata. Gothae.

Bridel, S.E. 1826. Bryologia universa seu systematica ad novam methodum dispositio, historia et descriptio omnium muscorum frondosorum hucusque cognitorum cum synonymia et auctoribus probatissimis. Lipsiae.

Briggs, D. 1965. Experimental taxonomy of some British species of the genus *Dicranum*. *New Phytol*. 64: 366-386.

Briggs, D. 1965b. The ecology of four British *Dicranum* species. *J. Ecol*. 53: 69-95.

Brotherus, V.F. 1906. Musci in Die Naturlichen Pflanzenfamilien by Engler & Prantl. Band II. Leipzig.

Brotherus, V.F. 1924. Musci in Die Naturlichen Pflanzenfamilien by Engler & Prantl. Ed. 2. Band X. Leipzig.

Bruch, P., W.P. Schimper and T. Gümbel. 1836-1855. Bryologia Europaea, seu Genera Muscorum Europaeorum Monographice Illustrata. Stuttegart.

Bryan, V.S. 1956. Chromosomes and systematic positions of the inoperculate mosses, *Pleuridium* and *Bruchia*. *Amer. J. Bot*. 43: 460-468.

Cain, S.A. 1944. Foundations of plant geography. New York.

Cardot, J. 1899. Études sur la flore Bryologique de l'Amerique du Nord. Revision des Types d'Hedwig et de Schwaegrichen. *Bull. Herb. Boissier* 7(4): 300-336.

Carlquist, S. 1974. Island biology. Columbia Univ. Press, New York.

Carmichael, J.M. 1978. The taxmap classification program, Version 3.1 - May, 1978. Mimeo, Univ. of Alberta, Edmonton.

Carmichael, J.M. and P.H.A. Sneath. 1969. Taxometric maps. *Syst. Zool.* 18: 402-415.

Carmichael, J.M., J.A. George and R.S. Julius. 1968. Finding natural clusters. *Syst. Zool.* 17: 144-150.

Chopra, R.S. and P.D. Sharama. 1958. Cytomorphology of the genus *Pogonatum* Palis. *Phytomorphology* 8: 41-66.

Chrobak, B. and A.J. Sharp. 1965. A preliminary comparative study of asexual reproduction in *Dicranum flagellare* and *Dicranum montanum*. *J. Hattori Bot. Lab.* 28: 122-128.

Coulter, H.W. *et al.* 1962. U.S. Geol. Survey Misc. Geol. Inv. Map I-415.

Crosby, M.R. and R.E. Magill. 1977. A dictionary of Mosses. Missouri Bot. Garden publ., St. Louis.

Crum, H.A. 1951. The Appalachian-Ozarkian element in the moss flora of Mexico with a check-list of all known Mexican mosses. Univ. of Michigan Doctoral Dissertation Series, Publ. No. 3486.

Crum, H.A. 1963. *Encalypta brevicolla* and *E. longicolla* in North America. Bull. Natl. Mus. Canada 186: 36-44.

Crum, H.A. 1966. Evolutionary and phytogeographic patterns in the Canadian moss flora, pp. 28-42 *in* R.L. Taylor and R.A. Ludwig (eds.). The Evolution of Canada's Flora. Univ. of Toronto Press, Toronto.

Crum, H.A. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. *J. Hattori Bot. Lab.* 35: 269-298.

Crum, H.A. 1973. Mosses of the Great Lakes forest. Contributions Univ. Michigan Herb. 10: 1-404.

Crum, H.A., W.C. Steere and L.E. Anderson. 1973. A new list of Mosses of North America North of Mexico. *Bryologist* 76: 85-130.

Crundwell, A.C. 1970. Notes on the nomenclature of British mosses. I. *Trans. Brit. Bryol. Soc.* 6(1): 133-138.

Culmann, M.P. 1920. Notes sur les Dicranacées et en particulier sur le Memoire de M.I. Hagen sur cette famille. *Bull. Soc. Bot. France* 67: 198-207.

Dalby, D.H. 1959. Polysety in *Polytrichum formosum*. *Trans. Brit. Bryol. Soc.* 3: 608-609.

Delgadillo, M.C. 1975. Taxonomic revision of *Aloina*, *Aloinella* and *Crossidium* (Musci). *Bryologist* 78: 245-303.

Dickson, J.H. 1967. *Pseudoscleropodium purum* (Limpr.) Fleisch. on St. Helena and its arrival on Tristan de Cunha. *Bryologist* 70: 267-268.

Dietz, R.S. and J.C. Holden. 1970. The breakup of Pangaea. *Sci. Amer.* 222(10): 30-41.

Dillenius, J.J. 1741. Historia muscorum in qua circiter sexcentae species veteres et novae ad sua genera relatae describuntur et iconibus genuinis illustrantur: cum appendice et indice synonymorum. Oxonii.

Du Rietz, G.E. 1940. Problems of bipolar plant distribution. *Acta. Phytogeogr. Suec.* 13: 215-282.

Farris, J.S. 1970. Methods for computing Wagner Trees. *Syst. Zool.* 19: 83-92.

Fernald, M.L. 1925. Persistence of plants in unglaciated areas of boreal America. *Mem. Amer. Acad. Arts* 15: 239-342.

Flowers, S. 1973. Mosses: Utah and the West. A. Holmgren (ed.). Brigham Young Univ. Press, Provo.

Gelting, P. 1934. Studies on the vascular plants of East Greenland between Franz Joseph Fjord and Dove Bay (Lat. 73°15' - 76°20'N). *Meddel. Grønland* 101: 2.

Gradstein, S.R. 1975. A taxonomic monograph of the genus *Acrolejunea* (Hepaticae). *Bryophytorum Bibliotheca* 4: 1-162. 24 plates.

Grout, A.J. 1937. Moss Flora of North America North of Mexico. 1(2): 63-135. Newfane, Vermont.

Hagen, I.S. 1915. Norges Dicranaceae. K. Norske Vidensk. Selsk. Skr. 1914(1): 1-192.

Hampe, E. 1867. *Ditrichum* Timm. statt *Leptotrichum* Hpe. *Flora* 50(12): 181-182.

Hedwig, J. 1782. Fundamentum historiae naturalis muscorum frondosorum concernens eorum flores, fructus, seminalem propagationem adiecta generum dispositione methodica, iconibus illustratis. Lipsiae.

Hedwig, J. 1801. Species Muscorum Frondosorum. Leipzig.

Hegewald, E. 1968. Untersuchungen zur verbreitungsbiologie einiger Moose I. *Dicranum scoparium* f. *saltans*. *Herzogia* 1: 19-24.

Hegewald, E. 1972a. *Dicranum tauricum* Sap. I. Die verbreitung in der Bundesrepublik Deutschland und angrenzenden gebieten. *Herzogia* 2: 335-348.

Hegewald, E. 1972b. Über das vorkommen der Laubmoose *Dicranum tauricum* und *Dicranum viride* in Nordrhein-Westfalen. *Naturw. Mitteilungen* 6: 35-44.

Hegewald, E. 1972c. *Dicranum groenlandicum* in Finnland. *Memoranda Soc. Fauna Fl. Fenn.* 48: 85-87.

Hennig, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.

Hennig, W. 1965. Phylogenetic systematics. *Ann. Rev. Entomology* 10: 97-116.

Hennig, W. 1966. Phylogenetic systematics. Univ. of Illinois Press, Urbana.

Hicklenton, P.R. and W.C. Oechel. 1976. Physiological aspects of the ecology of *Dicranum fuscescens* in the subarctic. I. Acclimation and acclimation potential of CO_2 exchange in relation to habitat, light, and temperature. *Canad. J. Bot.* 54: 1104-1119.

Holmen, K. 1958. Cytotaxonomical studies in some Danish mosses. *Bot. Tidsskr.* 54: 23-43.

Holzinger, J.M. 1925. Dr. Brotherus' Treatment of *Dicranum*. *Bryologist* 28: 22.

Horton, D.G. 1978. *Bryobrittonia longipes*, an earlier name for *B. pellucida* (Encalyptaceae; Musci). *Brittonia* 30: 16-20.

Horton, D.G. and B.M. Murray. 1976. *Encalypta brevipes* and *E. mutica*, gymnostomous species new to North America. *Bryologist* 79: 321-331.

Horton, D.G. and D.H. Vitt. 1976. Morphological characters, relative to distribution, and taxonomic considerations of the genus *Climacium* in North America. *Canad. J. Bot.* 54: 1872-1883.

Hultén, E. 1937. Outline of the history of arctic and boreal biota during the Quaternary Period. Bokförlags Aktiebolaget, Thule.

Hultén, E. 1968. Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford Univ. Press, Stanford.

Iltis, H.H. 1959. Studies in the Capparidaceae - VI *Cleome* sect. *Physostemon*. *Brittonia* II: 123-162.

Ireland, R.R. 1965. *Dicranum pallidisetum* in Western North America. *Bryologist* 68: 446-450.

Ireland, R.R. 1967. Chromosome studies on mosses from the state of Washington. II. *Bryologist* 70: 335-338.

Ireland, R.R. 1969a. Taxonomic studies on the genus *Atrichum* in North America. *Canad. J. Bot.* 47: 353-368.

Ireland, R.R. 1969b. A taxonomic revision of the genus *Plagiothecium* for North America, North of Mexico. Canadian National Museum of Nat. Sci. Publ. in Bot. I: 1-118.

Isoviita, P. 1977. On *Dicranum drummondii* and *D. ontariense* (Musci). *Ann. Bot. Fenn.* 14: 153-156.

Iwatsuki, Z. 1958a. Correlation between the moss flora of Japan and of the Southern Appalachians. *J. Hattori Bot. Lab.* 20: 304-352.

Iwatsuki, Z. 1958b. Two interesting *Fissidens* species common to Japan and eastern North America. *J. Jap. Bot.* 33: 245-250.

Iwatsuki, Z. 1972. Distribution of bryophytes common to Japan and the United States *in* Graham, A. (ed.). Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Publ. Co., Amsterdam. pp. 107-137.

Iwatsuki, Z., D.H. Vitt and S.R. Gradstein. 1976. Bryological Herbaria. A guide to the Bryological Herbaria of the world. *Bryophytorum Bibliotheca* 8: 1-144.

Iwatsuki, Z. and A.J. Sharp. 1967. The bryogeographical relationships between eastern Asia and North America. I. *J. Hattori Bot. Lab.* 30: 152-170.

Iwatsuki, Z. and A.J. Sharp. 1968. The bryogeographical relationships between eastern Asia and North America. II. *J. Hattori Bot. Lab.* 31: 55-58.

Jamieson, D.W. 1976. A monograph of the genus *Hygrohypnum* Lindb. (Musci). Univ. of British Columbia, Ph.D. Thesis.

Jensen, C. 1939. Skandinaviens Bladmossflora. Köpenhamn.

Karzmarz, K. 1971. A monograph of the genus *Calliergon* (Sull.) Kindb. *Monogr. Bot.* 34: 1-209.

Kindberg, N.C. 1889. Description of new species of mosses found at Ottawa. *Ottawa Naturalist* 2: 154-156.

Kindberg, N.C. 1890. New Canadian mosses. Described by Dr. Nils C. Kindberg, Linkoping, Sweden, 1889. *Ottawa Naturalist* 4: 61-65.

Kindberg, N.C. 1896. New or less known species of acrocarpous mosses from North America and Europe. *Rev. Bryol.* 23: 17-23.

Kindberg, N.C. 1897. Genera of European and North American Bryineae. Part II. Acrocarpus. Linkoping Lithografiska Aktibobg.

Kindberg, N.C. 1905. New North American Bryineae. *Rev. Bryol.* 32: 33-38.

Kindberg, N.C. 1910. Bryological notes. *Rev. Bryol.* 37: 13-15.

Klepper, B. 1963. Water relations of *Dicranum scoparium*. *Bryologist* 66: 41-54.

Koponen, T. 1968a. Generic revision of Mniaceae Mitt. (Bryophyta). *Ann. Bot. Fenn.* 5: 117-151.

Koponen, T. 1968b. On polysety in *Plagiomnium* Kop. sect. *Rosulata* (Kindb.) Kop. (Bryophyta). *Memoranda Soc. Fauna Fl. Fenn.* 44: 24-32.

Koponen, T. 1973. *Rhizomnium* (Mniaceae) in North America. *Ann. Bot. Fenn.* 10: 1-26.

La Roi, G.H. and M.H.L. Stringer. 1976. Ecological studies in the boreal spruce-fir forests of the North American Taiga. II. Analysis of the bryophyte flora. *Canad. J. Bot.* 54: 619-643.

Lawton, E. 1960. *Pseudoscleropodium purum* in the Pacific Northwest. *Bryologist* 63: 235-237.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Nichinan, Japan.

Lewinsky, J. 1977. The genus *Orthotrichum*. Morphological studies and evolutionary remarks. *J. Hattori Bot. Lab.* 43: 31-61.

Limpricht, K.G. 1890. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Leipzig.

Lindberg, S.O. 1865. Adnotationes Bryologicae. *Bot. Not.* 4: 78-80.

Lindberg, S.O. and H.W. Arnell. 1890. Musci Asiae Borealis. II. Laubmoose. *K. Svenska Vet. akad. Handl.* 28: 1-163.

Loeske, L. 1910. Studien zur vergleichenden Morphologie und phylogenetischen. Systematik der Laubmoose. Berlin.

Longton, R.E. 1962. Polysety in the British Bryophyta. *Trans. Brit. Bryol. Soc.* 4: 326-333.

Löve, A. and D. Löve. 1953. Studies in *Bryoxiphium*. *Bryologist* 56: 73-94, 183-203.

Löve, A. and D. Löve. 1975. Cytotaxonomical atlas of the arctic flora. Cramer publ., Liechtenstein.

Loveland, H.F. 1956. Sexual dimorphism in the moss genus *Dicranum* Hedw. (Univ. Microfilms). Ann Arbor.

Maass, W.S.G. 1965. Zur Kenntnis des *Sphagnum angermanicum* in Europa. *Svensk. Bot. Tidskr.* 59: 332-344.

Maass, W.S.G. 1966. Studies on the taxonomy and distribution of *Sphagnum*. I. *Sphagnum pylaesii* and *Sphagnum angermanicum* in Quebec and some phytogeographic considerations. *Bryologist* 69: 95-100.

Maass, W.S.G. 1967. Studies on the taxonomy and distribution of *Sphagnum*. IV. *Sphagnum majus*, *Sphagnum annulatum*, *Sphagnum mendocinum* and *Sphagnum obtusum* in North America. *Nova Hedwigia* 14: 187-214.

Macoun, J. 1889. Contributions to the bryology of Canada. *Bull. Torrey Bot. Club* 16: 91-98.

Macoun, J. 1890a. Contributions to Canadian bryology. 2. *Bull. Torrey Bot. Club* 17: 83-90.

Macoun, J. 1890b. List of mosses collected in the neighborhood of Ottawa. *Ottawa Nat.* 3: 149-152.

Macoun, J. 1922. Autobiography of John Macoun, M.A., Canadian explorer and naturalist, Assistant Director and Naturalist to the Geological Survey of Canada, 1831-1920. With introduction by Ernest Thompson Seton. A memorial volume published by the Ottawa Field-Naturalist's Club. Ottawa.

Macoun, J. and N.C. Kindberg. 1892. Catalogue of Canadian Plants. Part 6. Musci. Montreal.

Margadant, W.D. 1968. Early Bryological Literature. Pittsburgh.

Miller, H.A. 1971. An overview of the Hookeriales. *Phytologia* 21: 243-252.

Miller, N.G. 1976. Quaternary fossil bryophytes in North America: A synopsis of the record and some phytogeographic implications. *J. Hattori Bot. Lab.* 41: 73-85.

Mitten, W. 1869. Musci austro-americani. Enumeratio muscorum omnium austro-americanorum auctori huqusque cognitorum. *J. Linn. Soc. Bot.* 12: 1-659.

Mizushima, U. 1970. On *Dicranum drummondii* and *D. elatum*. *J. Jap. Bot.* 45: 155-160.

Moss, E.H. and G.H. Turner. 1961. Bryophytes from the Edmonton region, Alberta. *Canad. J. Bot.* 39: 1177-1193.

Müller, C. 1848-1849. Synopsis Muscorum Frondosorum Omnium Hucusque Cognitorum. I. Musci Vegetationis Acrocarpicae. Berlin.

Müller, C. 1901. Genera muscorum frondosorum. Classes Schistocarporum, Cleistocarporum, Stegocarporum complectenia, exceptis Orthotrichaceis et Pleurocarpis. Gattungen und Gruppen der Laubmoose in historischer und systematischer Beziehung, sowie nach ihrer geographischen Verbreitung unter Berücksichtigung der Arten. Mit einem Vorworte von Dr. Karl Schliephacke. Leipzig.

Nyholm, E. 1954. Illustrated Moss Flora of Fenoskandia. Fas. I. 1-87. Lund.

Packer, J.G. and D.H. Vitt. 1974. Mountain Park: A plant refugium in the Canadian Rocky Mountains. *Canad. J. Bot.* 52: 1393-1409.

Persson, H. 1947. Further notes on Alaskan-Yukon bryophytes. *Bryologist* 50: 279-310.

Persson, H. 1952. Critical or otherwise interesting bryophytes from Alaska-Yukon. *Bryologist* 55: 1-25, 88-116.

Persson, H. 1954. Mosses of Alaska-Yukon. *Bryologist* 57: 189-216.

Peterson, W.L. 1977a. Clarification of the nomenclature of *Dicranum condensatum*. *Bryologist* 80: 365-368.

Peterson, W.L. 1977b. *Dicranum ontariense* Peterson: a new name for a North American endemic moss. *Canad. J. Bot.* 55: 986-991.

Peterson, W.L. and J.M. Mayo. 1975. Moisture stress and its effect on photosynthesis in *Dicranum polysetum*. *Canad. J. Bot.* 53: 2897-2900.

Podpera, J. 1954. Conspectus Muscorum Europearum. Prague.

Porsild, A.E. 1958. Geographical distribution of some elements in the flora of Canada. *Geogr. Bull.* 11: 57-77.

Prest, V.K. 1969. Retreat of Wisconsin and recent ice in North America. Geol. Survey of Canada, Map 1257a.

Reimers, H. 1938. *Dicranum fulvum* Hook. und *D. viride* (Sull. *et* Lesq.) Lindb. *Hedwigia* 77: 261-293.

Renauld, M.F. 1901. Nouvelle classification des *Leucolonia*. *Rev. Bryol.* 28: 66-70, 85-87.

Renauld, F. and J. Cardot. 1888. Notice sur quelques mousses de l'Amerique du Nord. *Revue Bryol.* 15: 69-72.

Renauld, F. and J. Cardot. 1889. New mosses of North America. II. *Bot. Gaz.* 14: 91-100.

Ritchie, J.C. 1956. A plant collection from northwestern Manitoba. *Canad. Field-Naturalist* 70: 171-181.

Röll, J. 1896. Nachtrag zu der in der Hedwigia (Bd. XXXII 1893) erschienenen Arbeit über die von mir im Jahre 1888 in Nord-Amerika gesammelten Laubmoose. *Hedwigia* 35: 58-72.

Rowe, S.J. 1972. Forest Regions of Canada. Dept. of the Environment, Canadian Forestry Service Pub. 1300.

Sainsbury, G.O.K. 1942. Northern mosses in New Zealand. *Bryologist* 45: 40-43.

Sainsbury, G.O.K. 1955. A handbook of the New Zealand mosses. *Bull. Roy. Soc. New Zealand* 5: 1-490.

Sapehin, A.A. 1911. Laubmoose des Krimgebirges in ökologischer, geographischer und floristischer Hinsicht. *Bot. Jahrb. Syst.* 105: 1-36.

Savicz-Ljubitzkaja, L.I. and Z.N. Smirnova. 1970. The handbook of the mosses of the U.S.S.R. The mosses acrocarpous. Leningrad.

Sayre, G. 1959. Dates of publications describing Musci. 1801-1821. Troy, New York.

Schimper, W.P. 1856. Corollarium bryologiae europaea. Stuttgart.

Schofield, W.B. 1965. Correlations between the moss floras of Japan and British Columbia, Canada. *J. Hattori Bot. Lab.* 28: 17-42.

Schofield, W.B. 1966. *Crumia*, a new genus of the Pottiaceae endemic to western North America. *Canad. J. Bot.* 44: 609-614.

Schofield, W.B. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. *Madroño West Am. J. Bot.* 20: 155-207.

Schofield, W.B. 1972. Bryology in arctic and boreal North America and Greenland. *Canad. J. Bot.* 50: 1111-1133.

Schofield, W.B. 1974. Bipolar disjunctive mosses in the southern hemisphere, with particular reference to New Zealand. *J. Hattori Bot. Lab.* 38: 13-32.

Schofield, W.B. and H.A. Crum. 1972. Disjunctions in Bryophytes. *Ann. Missouri Bot. Gard.* 59: 174-202.

Schuster, R.M. 1959. Hepaticae *in* R.M. Schuster, W.C. Steere and J.W. Thompson. The terrestrial cryptogams of northern Ellesmere Island. *Bull. Nat. Mus. Canada* 165: 15-71.

Schuster, R.M. 1969. Problems of antipodal distribution in lower land plants. *Taxon* 18: 46-91.

Schwaegrichen, F. 1823. (Species Muscorum, Hedwig) Opus posthumum supplementum Primum scriptum. Suppl. 2(I). Leipzig.

Scott, A.M., I.G. Stone and C. Rosser. 1976. The Mosses of Southern Australia. Academic Press, London.

Seki, T. 1968. A revision of the family Sematophyllaceae of Japan with special reference to statistical demarcation of the family. *J. Sci. Hiroshima Univ., Ser. B., Div. 2(Bot.)* 12: 1-80.

Seltzer, R.C. and W.A. Wistendahl. 1971. Some environmental factors related to the occurrence of *Dicranum fulvum* in southeastern Ohio. *Bryologist* 74: 28-32.

Sharp, A.J. 1939. Taxonomic and ecological studies of eastern Tennessee bryophytes. *Amer. Midl. Naturalist* 21: 267-354.

Sharp, A.J. 1941. Some historical factors and the distribution of southern Appalachian bryophytes. *Bryologist* 44: 16-18.

Sharp, A.J. 1966. Some aspects of Mexican phytogeography. *Ciencia (Mexico)* 24: 229-232.

Sharp, A.J. 1971. Epilogue *in* P.C. Holt (ed.). The distributional history of the biota of the Southern Appalachians. Part II. Flora Res. Div. Monogr. 2. Va. Poly. Inst. & State Univ., Res. Div. Monograph 2: 405-410.

Sharp, A.J. and Z. Iwatsuki. 1965. A preliminary statement concerning mosses common to Japan and Mexico. *Ann. Missouri Bot. Gard.* 52: 452-456.

Smith, G.L. 1971. A conspectus of the genera of Polytrichaceae. *Mem. New York Bot. Gard.* 21(3): 1-83.

Smith, J.E. 1804. Flora Britannica. Vol. III. London.

Snider, J. 1970. Chromosome studies of some mosses of the Douglas Lake region. *Michigan Bot.* 9: 67-71.

Sokal, R.R. and P.H.A. Sneath. 1963. Principles of numerical taxonomy. W.H. Freeman & Co., San Francisco.

Sowter, F.A. 1948. The polysetous inflorescence of *Dicranum majus* L. *Trans. Brit. Bryol. Soc.* 1: 73-74.

Stafleu, F.A. *et al.* 1972. International Code of Botanical Nomenclature. pp. 1-79. Utrecht.

Stebbins, G.L. 1971. Chromosomal evolution in higher plants. Arnold Publ. Ltd., London.

Steere, W.C. 1937. *Bryoxiphium norvegicum*, the sword moss, as a preglacial and interglacial relic. *Ecol.* 18: 346-358.

Steere, W.C. 1947. A consideration of the concept of genus in Musci. *Bryologist* 50: 247-258

Steere, W.C. 1953. On the geographical distribution of arctic bryophytes. pp. 30-47 *in* I.L. Wiggins, Current Biological Research in the Alaskan Arctic (Stanford Univ. Publ. Univ. Series, Biol. Sci., Vol. II).

Steere, W.C. 1954. Chromosome number and behaviour in arctic mosses. *Bot. Gaz.* 116: 93-133.

Steere, W.C. 1963. The geographic distribution of *Funaria polaris*. *Bryologist* 66: 213-217.

Steere, W.C. 1965. The boreal bryophyte flora as affected by Quaternary glaciation *in* Wright, A.E. and D.G. Frey (eds.). The Quaternary of the United States. Princeton Univ. Press, Princeton.

Steere, W.C. 1969. Asiatic elements in the bryophyte flora of western North America. *The Bryologist* 72: 507-512.

Steere, W.C. 1972. Chromosome numbers in bryophytes. *J. Hattori Bot. Lab.* 35: 99-125.

Steere, W.C. 1974. The status and geographical distribution of *Voitia hyperborea* in North America (Musci: = Splachnaceae). *Bull. Torrey Bot. Club* 101: 55-63.

Steere, W.C. 1978. The mosses of Arctic Alaska. *Bryophytorum Bibliotheca* 14: 1-508.

Steere, W.C. and G.R. Brassard. 1974. The systematic position and geographical distribution of *Fissidens articus*. *Bryologist* 77: 195-202.

Steere, W.C. and B.M. Murray. 1974. The geographical distribution of *Bryum wrightii* in arctic and boreal North America. *Bryologist* 77: 172-178.

Steere, W.C., G.W. Scotter and K. Holmen. 1977. Bryophytes of Nahanni National Park and vicinity, Northwest Territories, Canada. *Canad. J. Bot.* 55: 1741-1767.

Størmer, P. 1969. Mosses with a Western and Southern Distribution in Norway. Oslo.

Sullivant, W.S. 1849. Contributions to the bryology and hepaticology of North America. Part II. Mem. Amer. Acad. Arts and Sci. New Series 4: 169-176.

Sullivant, W.S. 1856. The Musci and Hepaticae of the United States east of the Mississippi River *in* Gray's manual of botany. 2nd ed. Ivison & Phinney, New York.

Takaki, N. 1964. A revision of Japanese *Dicranum*. *J. Hattori Bot. Lab.* 27: 73-123.

Takaki, N. 1966. A revision of Japanese *Dicranoloma*. *J. Hattori Bot. Lab.* 29: 214-222.

Takaki, N. 1972. Geographical distribution of Japanese *Dicranum* species in the Northern Hemisphere. *J. Hattori Bot. Lab.* 35: 31-40.

Tarkhova, T.N. 1970. The influence of soil factors on the development of mosses. *Ekologiya* 4: 30-39.

True, R.H. 1899. Geographical distribution of Dicrana. *Bryologist* 2: 25-27.

Tuomikoski, R., T. Koponen and T. Ahti. 1973. The mosses of the island of Newfoundland. *Ann. Bot. Fenn.* 10: 217-264.

Turner, D. 1804. Muscologiae Hibernicae spicilegium. Yarmouth.

Vaarama, A. 1950a. Accessory isochromosomes in the moss species *Dicranum majus*. *Nature* 165: 894.

Vaarama, A. 1950b. Studies on chromosome numbers and certain meiotic features of several Finnish moss species. *Bot. Not.* 1950: 239-256.

Valanne, N., S. Toivonen and R. Saarinen. 1976. Ultrastructural changes in germinating *Dicranum scoparium*: A moss containing protein storage material. *Bryologist* 79: 188-198.

van Zanten, B.O. 1976. Preliminary report on germination experiments designed to estimate the survival chances of moss spores during aerial trans-oceanic long-range dispersal in the Southern Hemisphere, with particular reference to New Zealand. *J. Hattori Bot. Lab.* 41: 133-140.

Vitt, D.H. 1971. The infrageneric evolution, phylogeny, and taxonomy of the genus *Orthotrichum* (Musci) in North America. *Nova Hedwigia* 21: 683-711.

Vitt, D.H. 1973. A revision of the genus *Orthotrichum* in North America, North of Mexico. *Bryophytorum Bibliatheca* I: 1-208.

Vitt, D.H. 1974a. The distribution of *Bryobrittonia pellucida* Williams (Musci). *Arctic* 27: 237-241.

Vitt, D.H. 1974b. A key and synopsis of the mosses of Campbell Island, New Zealand. *New Zealand J. Bot.* 12: 185-210.

Vitt, D.H. 1975. A key and annotated synopsis of the mosses of the northern lowlands of Devon Island, N.W.T., Canada. *Canad. J. Bot.* 53(19): 2158-2197.

Vitt, D.H. 1976. The genus *Seligeria* in North America. *Lindbergia* 3: 241-275.

Vitt, D.H. and R.E. Andrus. 1975. *Sphagnum aongstroemii* in North America. *Bryologist* 79: 463-467.

Vitt, D.H. and R.E. Andrus. 1977. The genus *Sphagnum* in Alberta. *Canad. J. Bot.* 55: 331-357.

Vitt, D.H. and C.D. Hamilton. 1975. Taxonomic status of *Tomenthypnum falcifolium*. *Bryologist* 78: 168-177.

Wagner, W.H., Jr. 1952. The fern genus *Diellia*. *Univ. Calif. Publ. Bot.* 26: 1-212.

Wagner, W.H., Jr. 1962. *In* Benson, L. Plant taxonomy. Methods and Principles. pp. 273-277, 415-417. New York.

Weber, W.A. 1960. A second American record for *Oreas martiana*, from Colorado. *Bryologist* 63: 241-244.

Weber, W.A. 1965. Plant geography in the southern Rocky Mountains *in* Wright, H.E., Jr. and D.G. Frey (eds.) The Quaternary of the United States. Princeton Univ. Press. pp. 453-468.

Weber, W.A. 1973. Guide to the mosses of Colorado. Keys and ecological notes based on field and herbarium studies. Inst. Arctic & Alpine Research, Univ. Colorado Occasional Paper 6: 1-48.

Whittier, H.O. 1976. Mosses of the Society Islands. Univ. of Florida Press. Gainesville.

Wijk Van der, R., W. . Margadant and P.A. Florschutz. 1962. Index Muscorum. Vol. II. Utrecht.

Williams, R.S. 1913. Dicranaceae. *N. Am. Flora* 15(2): 77-166.

Yano, K. 1950. On chromosomes in some mosses. *Bot. Mag. (Tokyo)* 63: 224-225.

Yano, K. 1951. On the chromosomes in somes mosses. I. *Bot. Mag. (Tokyo)* 64: 234-237.

Yano, K. 1954. On the chromosomes in some mosses. VII. Chromosomes in two genera of Polytrichaceae and eight other genera. *Bot. Mag. (Tokyo)* 67: 243-246.

Yano, K. 1957. Cytological studies on Japanese mosses. I. Fissidentales, Dicranales, Grimmiales, Eubryales. The Kyoiku-kagaku [Mem. Faculty of Educ. Niigata Univ.] 6: 1-31.